FEEDING HABITS OF FOURTEEN EUROPEAN FRESHWATER FISH SPECIES

by

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ABSTRACT. - In this study we attempt to develop a synthesis of previously published work concerning the feeding habits of fourteen European freshwater fish: *Anguilla anguilla* L., *Salmo trutta* L., *Rutilus rutilus* L., *Leuciscus leuciscus* L., *Leuciscus cephalus* L., *Phoxinus phoxinus* L., *Gobio gobio* L., *Abramis brama* L., *Cyprinus carpio* L., *Tinca tinca* L., *Barbatula barbatula* L., *Gasterosteus aculeatus* L., *Perca fluviatilis* L. and *Cottus gobio* L. Data presented in this paper were obtained from 98 studies in 16 European countries. Great Britain with 40 studies was the most documented country. In order to synthetize the maximum information for each species, all methods used for analysing feeding habits and found in the different studies have been taken into account. Results are presented on tables with a commentary for each species analysed. The fourteen species were then classified into major trophic guilds.

RÉSUMÉ. - Cet article représente une synthèse bibliographique du régime alimentaire de 14 espèces de poissons d'eau douce européens: *Anguilla anguilla* L., *Salmo trutta* L., *Rutilus rutilus* L., *Leuciscus leuciscus* L., *Leuciscus cephalus* L., *Phoxinus phoxinus* L., *Gobio gobio* L., *Abramis brama* L., *Cyprinus carpio* L., *Tinca tinca* L., *Barbatula barbatula* L., *Gasterosteus aculeatus* L., *Perca fluviatilis* L., et *Cottus gobio* L. Les données analysées ont été extraites de 98 études réalisées dans 16 pays. La Grande Bretagne, avec 40 études, reste le pays le plus documenté en matière de régime et de comportement alimentaire des poissons d'eau douce. Afin de répertorier le maximum d'information sur chacune des espèces, toutes les méthodes d'analyse des contenus stomacaux ont été prises en compte. Les résultats sont présentés sous forme de tableaux synthétiques et un résumé est effectué pour chacune des espèces analysées. Les quatorze espèces ont été classées ultérieurement en guildes trophiques.

Key-words. - Freshwater fish, Europe, Food Habits, Trophic Guild.

Food habit studies are an important way to understand mechanisms and processes which structure fish assemblages (Kortrschal and Thomson, 1986; Gershanovich and Taufik, 1992). Analysing feeding patterns can contribute to an understanding of the interaction between members of these assemblages. In addition, knowledge of prey selection enables assessment of the energy base and the trophic dynamics of the stream community (Hartley, 1948; Miller *et al.*, 1988).

The objective of this study, based on an extensive literature review, is to describe the feeding habits of fourteen European freshwater fish species. As the food resource used often varies with the stage of life cycle, this synthesis is restricted to the adult period of fish. Furthermore, the availability of food organisms is also related to local, seasonal and

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diurnal changes and thus determine the dynamics of the quantitative composition of the food available to fish.

This review brings together dispersed information concerning all these variables, and presents a synthetic picture of fish diet which could be used as a base for the establishment of trophic guilds, and for basic research on resource partitioning, competition, habitat selection, and aquatic life management.

MATERIALS AND METHODS

Data presented in this paper were obtained from 98 studies in 16 European countries. Great Britain with 40 studies was the most documented country (Table I). In order to synthetize the maximal information for each species, all methods used for analysing feeding habits and found in the different studies have been taken into account. Most papers used one or more of the following four measures: (1) frequency of occurrence which is the proportion or percentage of fish guts in which a particular food item was found; (2) numerical abundance which is the number of individuals of a particular food item found in each gut or the percentage of all gut contents combined that the prey type comprised; (3) volumetric importance which is the percentage by volume or weight that a given prey type comprised in the total volume of all gut contents (some authors have opted to use only the dry prey items to avoid errors caused by the water trapped within the item); (4) the points method which is based on size of prey as well as their abundance; each category of food item is allotted a number of points proportional to the stomach fullness and the points gained by each food item are then summed and converted to percentages. As previously noted by Hynes (1950) and Hyslop (1980), any single measure by itself can be potentially mislead

Great Britain	40
France	12
Former Soviet Union	8
Poland	8
Ireland	7
Norway	5
Czechoslovakia	3
Sweeden	3
Finland	3
Germany	2
Denmark	2
Yugoslavia	1
Portugal	1
Austria	1
Rumania	1
Iceland	1
TOTAL	**98**

Table I. - Literature compiled from different works on feeding habits of 14 European freshwater fish species.

ing in some way. For example, frequency of occurrence information may be biased toward relatively scarce food items that occur often but do not contribute very much either in number or volume; numerical abundance is biased toward smaller food items, which, if commonly consumed by a fish predator, must be more numerous than large food items; volumetric or weight measures are biased toward larger items, which may take longer to digest.

Data concerning fish feeding behaviour were presented in very different forms depending on the study and consequently it was necessary to harmonise information by:

- the conversion of percentages illustrated by histograms into numerical tables;
- the modification of percentages where zero stomach contents were included (uniquely for the occurrence method);
- the annual synthesis of seasonal and monthly data;
- the selection of the most representative prey in stomach content analyses (prey only mentioned in less than 5% of studies were omitted);
- the choice of taxonomic unit most commonly used for each prey.

Diet was thus described based on 28 taxonomic varieties of which the systematic units are the Phylum, the Class, the Order or the Family.

Prey ingested by fish were described in detail in some studies and partially in others. To described the genus or species of prey, the percentages of the same taxonomic unit need simply to be added where percentages concern numerical abundance, volume, or weight. However this procedure can not be used in the frequency of occurrence method. For this method, where in the same taxonomic unit there exists several categories of prey, the actual percentage of this variety is somewhere between the maximum percentage of these categories and the sum of their percentages:

Maximum % of occurrence (Oim) < % of occurrence of the taxonomic unit (OTU) < sum of percentages of occurrence (Oi).

From several studies (Hartley, 1948; Thomas, 1962; Crivelli, 1979) where the authors supplied not only the percentages of occurrence for each category but also the true corresponding (OTU), it was possible to analyse the variation of this OTU between Oim and Oi according to the function:

$$f(\mathrm{Oim}) = \mathrm{OTU} - \mathrm{Oim} / \mathrm{Oi} - \mathrm{Oim}$$

Distribution of these points (Fig. 1) has permitted the establishment of a simple regression model :

$$f(\mathrm{Oim}) = 0{,}93 - 0{,}01\mathrm{Oim}$$

All the percentages of occurrence marked (*) in the tables have been calculated using this method.

We compiled a synthetic dietary data matrix (in frequency of occurrence) for the fourteen species analysed. The percent occurrence of the food items were first transformed into arcsine values. The final transformed Food Items-by-Fauna matrix was then analysed by a factor analysis, the factorial analysis of correspondences (FAC), using the ADE software package (Chessel and Dolédec, 1992). A taxonomic distance was computed from the coordinates of factors retained previously in the FAC analysis and using the euclidian distance. Distance values for the trophic matrix were then clustered with the unweighted pair-group method using arithmetic averages (e.g., UPGMA; Gauch, 1982), and summarized in a dendrogram grouping species with "similar" diet composition.

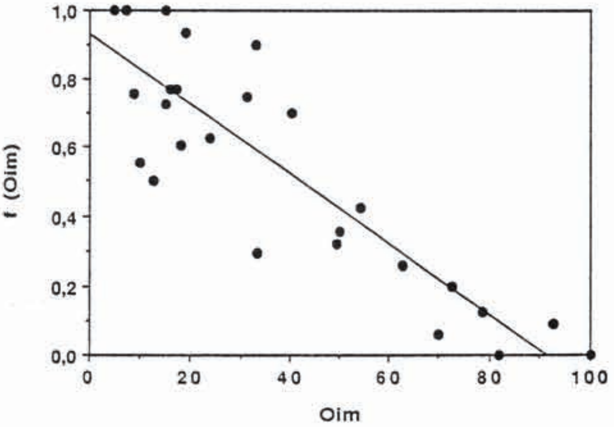

Fig. 1. - Variation of f(Oim) as a function of maximum percentage of occurrence (Oim). f(Oim) = (OTU-Oim)/(Oi-Oim). OTU = % of occurrence of the taxonomic unit; Oi = sum of percentages of occurrence; f(Oim) = 0.93 - 0.01 Oim.

RESULTS AND DISCUSSION

Feeding habits of the fourteen freshwater fish species analysed

The eel (*Anguilla anguilla* L.) (Table II)

The eel is a benthic fish with piscivorous tendancies. It feeds mainly at night (Deelder, 1984; Neveu, 1981a) from April to November (Bertin, 1956; Sinha and Jones, 1967). Low winter temperatures (< 10°C) largely inhibit its predatory activities (Bertin, 1956; Thomas, 1962; Sinha and Jones, 1967; Neveu, 1981a).

Unlike other benthic fish, the eel feeds on very few diptera larvae. Only Mann and Blackburn (1991) and Frost (1946) enumerated almost 50% similar organisms amongst prey ingested by the eel. However, ephemeropterans and trichopterans constitute its principal food. These two taxons alone represent 30 to 40% of its diet (Thomas, 1962; Sinha and Jones, 1967; Moriarty, 1974; Rasmussen and Therkildsen, 1979). Insect larvae are eaten from spring to summer (Sinha and Jones, 1967; Neveu, 1981a).

According to most work done on the subject, crustaceans are little sought after. However, particularly during autumn and winter (Rasmussen and Therkildsen, 1979; Mann and Blackburn, 1991), amphipods and isopods can become the eel's principal source of food (Schiemenz, 1910; Hartley, 1948; Moriarty, 1974; Rasmussen and Therkildsen, 1979; Neveu, 1981a).

The relationship between competition and predation of the eel and other fish, mainly salmonids, has been the subject of numerous papers. These have all maintained the idea of a voracious fish. Although competition with regard to salmonidae is not negligeable, particularly during summer (Sinha and Jones, 1967), close observation of respective diets reveals several marked differences in feeding strategies (Thomas, 1962; Mann and Blackburn, 1991). Predation on salmonid fry seems unlikely. Of 4340 eels examined by Sinha and Jones (1967) in 16 different English rivers, only 10 had ingested a salmonid. In other studies, salmonophagic eels represented only 1% (Frost, 1946; Jones and Evans, 1960; Thomas, 1962). The eel, however, manifests a clear preference for bullhead, *Cottus gobio* L. (Mann and Blackburn, 1991) or minnow, *Phoxinus phoxinus* L. (Thomas, 1962), and cannibalism appears to be quite common among this species (Hornyolds, 1926). Amongst fish examined by Sinha and Jones (1967) as many as 3% had ingested other eels. It would appear that fish play an important part in the eel's diet (Hartley, 1948; Thomas, 1962; Shafi and Maitland, 1972; Moriarty, 1975), even though according to Rogers (1966), Sinha and Jones (1967), Moriarty (1979), and Mann and Blackburn (1991) this fish is not highly piscivorous. On reaching 40 cm in length, the eel starts to feed regularly on other fish (Rasmussen, 1979; Mann and Blackburn, 1991).

The eel can also feed on fish eggs. Rasmussen and Therkildsen (1979) observed that in a Danish river, around 7% of the weight of food ingested over a year consisted of eggs. This feeding behavior, observed essentially in winter and spring, have not been observed elsewhere (Sinha and Jones, 1967). The eel is one of the few freshwater fish that predate shrimp and when shrimp are abundant large quantities are ingested (Hartley, 1948; Svardson, 1972; Mann and Blackburn, 1991).

Finally, some authors have reported unusual items in the diet of eels; Schiemenz (1910) observed large quantities of plankton in the stomach of eels, and Hornyolds (1926) describes frogs and chickens having been found by fishermen.

The brown trout (*Salmo trutta* L.) (Table III)

The trout is a diurnal and noctural predator (Heggenes *et al.*, 1993) feeding on a wide variety of benthic and surface prey. The majority of its diet is made up of insects (80%), mainly represented by trichopteran larvae, aerial or terrestrial insects and ephemeropteran larvae, respectively. In spite of a very specific diet, the trout does not appear to be particularly selective and feeds essentially on the most easily accessible prey (Slack, 1934; Neil, 1938; Frost and Smyly, 1952; Nilsson, 1955; Ball, 1961; Graham and Jones, 1962; Thomas, 1964; Egglishaw, 1967; Siddiqui, 1969; Hunt and Jones, 1972; Neveu and Thibault, 1977; Pedley and Jones, 1978; Neveu, 1981c; Valente and Heland, 1990). This notion of accessibility depends on size, mobility and habitat of the organisms. Thus, the trout's feeding strategy is based essentially on exploitation of drift of the most mobile benthic prey (Nilsson, 1955; Horton, 1961), and imagos surfacing at maturity (Frost, 1939; Straskrabra *et al.*, 1966). Because of this, oligochaets and hirundineans concealed in silt or under stones are largely protected from predation (Thomas, 1962).

Variation in the diets of trout as observed by Pentelow (1932), Ball (1961), Graham and Jones (1962), Thomas (1964), Mann and Orr (1969), and Neveu and Thibault (1977), is probably the result of variability in the relative abundance of organisms in the environment.

The trout is unaffected to temperature variation and feeds actively throughout the year (Thomas, 1962; Thomas, 1964; Egglishaw, 1967). Empty stomach contents, however, are more frequent in winter and Brown (1946) observed a correlation between increase in predation and increase in temperature.

The trophic specificity of both river and lake trout is characterized by a large consumption of surface insects (Tusa, 1969; Elliot, 1973). These insects were found in more than 60% of fish examined and made up around 20% of the trout's diet thus illustrating that the trout is the largest consumer of terrestrial and aerial insects with the salmon second (Frost, 1950; Thomas, 1962; Maitland, 1965; Mann and Orr, 1969; Tusa, 1969; Pedley and Jones, 1978). These prey are integrated into the trout's diet during April and by the end of summer and beginning of autumn become its main source of nutrition (Pentelow, 1932; Ball, 1961; Thomas, 1962; Maitland, 1965; Tusa, 1969; Neveu and Thibault, 1977). Egglishaw (1967) observed that by October as much as 90% of the weight of stomach contents was made up of surface insects with an average of almost 40% between May and

Table II a, b. - Feeding habits of the adult eel (*Anguilla anguilla* L.), expressed as percentage occurrence, percentage number, percentage volume, percentage weight and percentage point.

Study number	1a	1b	2	3	4a	4b	4c	4d	4e	4f	5	6	7
Sources	Frost (1946)		Hartley (1948)	Thomas (1962)	Sinha (1967)						Shafi (1972)	Moriarty (1974)	Moriarty (1975)
Countries	G B		G B	G B	G B						GB	IRELAND	IRELAND
Sites (lake/river)	l. Winderemere	r. Leven	r. Cam	r. Teify	r. Wen	r. Dwfach	r. Erch	r. Ffraw	r. Ogwen	r. Rhyd-hir	l.Dubh	l.Lough Key	r. Erne
Sampling dates				I- XII	I-XII (63-64)								
Nb stomachs examined	106	32	125	155	388	247	703	852	848	329	22	49	17
Nb of full stomachs	106*	32*	125*	155*	322	208	192	212	563	241	22*	49*	17*

* Authors did not mention the number of empty stomachs

Study number	1a	1b	2	3	4a	4b	4c	4d	4e	4f	5	6	7
Methods	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.
Chironomids (l/p)	7.5	31.5*	3.2	18.8	8	10	24	10	17	9	4	20	12
Simuliids (l/p)			5.6	10	2.3	2.5	15	7	8	3	14		
other Dipterans (l/p)					0.7	2.4	6	0.4	2	0.8			
Ephemeropterans (l/p)	11.8*	48*	13	70	27.9	27.4	76.5	15.1	21.1	9.1	9	43	6
Trichopterans (l/p)	31.9*	11.5*	4.6	46	19.8	38	100	25	61.8	36.1		10	59
Plecopterans (l/p)		15.6		30.7	13.5	11	29.2	8.5	35.2	11.2			
Coleopterans (l/a)			2	4	3.1	3.8	2.6	2.3	0.2	0.4			
Megalopterans (l/p)	12.2												
Heteropterans (a)		3.1							0.3				
Odonatans (l)	1.9												
Terrestrial insects (a)					1	2.4	0.5	0.9	0.7	0.2			
Total Insects	52.1*	74.9*	28.8	92.5*	58.5*	70.1*	100*	54.3*	88.1*	54.8*	24*	58*	65.1*
Decapods			26.4										
Amphipods	19.8		31	1.4	0.9	1.8		14	0.9	22		4	12
Isopods	0.9	9.5	1.6	4.2	0.9	1.5		10		9		47	47
Ostracods			0.8										
Total crustaceans	20.7*	9.5	48.5	5.5*	1.8	3.2	0	21.8	0.9	28.3*	0	48.9*	52.3*
Teleosts	0.9	3.1	22.4	24	24.8*	17*	10.9*	16.7*	4.2*	8.2*	24	2	65
Fish eggs							1.5			2.1			
Molluscs	79.6*		4.8*	20	0.3	13.5	9.3	7.1	4.6	17.4		44.2	29
Oligochets	2.9	6.2	1.6		9	4.8	12	13.2	6.2	8.7			
Hirudineans				24									
Algae			6.4										

(l/p) larvae and/or pupae; (l/a) larvae and/or adults; (a) adults; (l) larvae

*approximated % of occurrence

Study number	1a	1b	2	3	4a	4b	8	9a	9b	10
Sources	Frost (1946)		Hartley (1948)	Thomas (1962)	Sinha (1967)		Rasmussen (1979)	Neveu (1981b)		Mann (1991)
Countries	G B		G B	G B	G B		**DENMARK**	**FRANCE**		**G B**
Sites (lake/river)	l. Winderemere	r. Leven	r. Cam	r. Teify	r. Wen	r. Dwfach	r. Koge-Lellinge	r. Nivelle		r. Frome
Sampling dates				I-XII	I-XII (63-64)		IV-XII (71-74)	VI (76)	I-XII (74)	
Nb stomachs examined	106	32	1 25	155	388	247	6 18	131 (1)	335 (1)	1348
Nb of full stomachs	106*	32*	1 25*	155*	322	208	6 18*	95	335*	1348*

* Authors did not mention the number of empty stomachs

Study number	1a	1b	2	4a	4b	9a	9b	10	3	4a	4b	8
Methods	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% Points	% Vol.	% Vol.	% Weight
Chironomids (l/p)	1.9	63.1	1.1	14.7	4.4	1.7	1.6	5.2	2.2	0.6	0.2	5.8
Simuliids(l/p)			8	11.3	0.7	4.4		49.6	1	0.6		
other Dipterans (l/p)				0.4	1.9			0.2		0.1		
Ephemeropterans (l/p)	1.6	22.3	14.6	38.4	37	45.5	30.6	17.2	48.8	6.1	8.4	26.4
Trichopterans (l/p)	11.3	3.2	1.7	10.8	35.8	4.7	13	4.7	23.4	7.6	24.6	0.3
Plecopterans (l/p)		5.2		3.5	7		0.1		5.2	0.4	1.7	1.7
Coleopterans (l/a)			0.3				0.8	0.4				
Megalopterans (l/p)	1.9						1.1					
Heteropterans (a)		0.5					0.1					
Odonatans (l)	0.1						0.1					
Terrestrial insects (a)				0.6	0.9		1			0.4	0.6	
Total insects	**16.8**	**94.3**	**25.7**	**80**	**87.7**	**56.3**	**47.4**	**77.3**	**74.7**	**15.8**	**37.7**	**33.3**
Decapods			9.3									
Amphipods	7.3		49.1	0.1	1.2	42.4	49	9.4	1.6		0.2	
Isopods	0.2	4.1	0.4	6.4	2.7		1.4	5	1	1.7	0.3	32.1
Total crustaceans	**7.5**	**4.1**	**58.8**	**6.5**	**3.9**			**14.4**	**2.6**	**1.7**	**0.5**	**32.1**
Teleosts		0.5	3	4.1	2.3		0.2	4	15.6	69.5	33	6.8
Fish eggs												6.5
Molluscs	75		6.3	0.1	4.3		0.8	0.4	2.8		13.3	1.5
Oligochets	0.6	1.1	0.2	3.6	1.2		0.2	0.1		6.6	12.8	
Hirudineans									5.2			16.3

(l/p) larvae and/or pupae; (l/a) larvae and/or adults; (a) adults; (l) larvae

(1) 20 cm < individuals < 39.9 cm

Table III a, b. - Feeding habits of the adult brown trout (*Salmo trutta* L.), expressed as percentage occurrence, percentage number, percentage volume, percentage weight and percentage point.

Study number	1a	1b	2a	2b	3	4	5	6
Sources	Pentelow (1932)		Frost (1939)		Hartley (1948)	Frost (1950)	Nilson (1955)	Ball (1961)
Countries	G B		IRELAND		G B	GB	SWEDEN	G B
Sites (lake/river)	r. Tees	r. Itchen	r. Liffey	r. Liffey	r. Cam	r. Forss	l. Blasjön	l. Llyn Tegid
Sampling dates			I-XII	I-XII	I-XII (39-41)	VI-VII	IV-X (44-49)	I-XII (53)
Nb stomachs examined	104	29	124 (1)	121 (2)	3 0	74(3)	6 59*	2 53
Nb of full stomachs	101	27	124*	121*	3 0*	74*	6 59*	2 53*

Study number	7	8	9	10	11	12	13	14
Sources	Thomas (1962)	Crisp(1983)	Mills (1964)	Maitland (1965)	Sinha (1967)	Hunt (1972)	Pedley (1978)	Valente (1990)
Countries	G B	GB	GB	G B	GB	G B	GB	PORTUGAL
Sites (lake/river)	r. Teify	r. Tees	r. Bran	r. Endrick	r. Dwyfach	l. Llyn Alaw	l. Llyn Dwythwch	r. Estoràos
Sampling dates	I-XII	IV-VIII (60)		I-XII 61)	I-XII	I-XII (69-70)	I-XII	VII (84-85)
Nb stomachs examined	7 41	30 (4)	514	45 8	159	274	378	54 (5)
Nb of full stomachs	7 41*	27	514*	45 8*	159*	274*	378*	5 2

* Authors did not mention the number of empty stomachs

Study number	1a	1b	2a	2b	3	4	5	6	7	8	9	10	11	12	13	14
Methods	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.
Chironomids (l/p)	23.8		27.4	56.2		61.7*	24.9	11*	11.4	37	16	57.5*	41	20.2*	77.3*	36.5
Simuliids (l/p)	6.9		38.7*	40.1*	3.3	1	3		5.7			13	10.5		0.3	18.3
other Dipterans (l/p)			36.5*	46.3*		11	11.1					30*				18.3
Ephemeropterans (l/p)	39.6*	59.3*	69.3	57	23.7	85.7*	21.4	26	34	25.9	15	57*	35.5*		38.7*	51.9
Trichopterans (l/p)	47.3*	37	64.5*	88.1*	84	95.4*	58.4	52.6*	96	40.7	38	18.2*	57.3*	5.5*	98.6*	73.1
Plecopterans (l/p)	11.9*		20.2	62.8		4	15.5	21	44	40.7	17	38.1*	34.8*		1.8*	26.9
Coleopterans (l/a)	7.7		7.2	33	19.3	60.5*	12.3	4	8	7.4	11	15*	8.3*		15.4*	63.5
Megalopterans (l/p)					13.3	5	2	10	8					1.1		
Heteropterans (a)	6.7	29.6	4.8	7.4	16.2			5	9		10			77.5*	21.7*	
Odonatans (l)																13.5
Terrestrial insects (a)	83.2*	67.7*	100*	100*	70.4*	57*	77.9*	36	42.8	79.2*	30	97.3*	40.6*	8.5*	49.5*	59.6
Total insects	**92.9***	**100***	**100***	**100***	92.2	**100***	**96.1***	**96.4***	**100***	**95.1***	**90.9***	**100***	**100***	**81.8***	**100***	**100***
Decapods		29.6	13.7		10											
Amphipods	7.9	40.7	14.5		33	1	35.2	29	6.6		1	28		55.9	0.5	
Isopods			7.2				0.1	20	21.6				2.5	46.3		
Cladocerans						36	9.4	2							11.3*	
Ostracods														2.9		
Total crustaceans	7.9	55.7*			43.3	36.6*	40.5*	42.8*	26.2*	0	1	28	2.5	73*	11.8*	
Diatoms					3.3											
Algae					3.3		3.4									
Macrophytes					3.3											
Total plants	0	0			9.3*	0	3.4	0	0	0	0	0	0	0		
Teleosts	5.9		14.5	1.6	26.6		2.3	4	5.1	66.7	5		2.8	16.5	23	
Fish eggs								8	1.1					0.4	1.3	
Molluscs	3	36	19.3	3.3	13	13.1*	32.2*	4	14		3	3*	15.7*	12.5*	35*	
Oligochets	3		3.2	3.3	6.6		1					4*	8.1*	1.1		
Hirudineans														18.7		

(l/p) larvae and/or pupae; (l/a) larvae and/or adults; (a) adults; (l) larvae

*approximated % of occurrence

(1) 112 g < individuals < 560 g; (2) 56 g < individuals < 168 g; (3) average length of individuals: 12.6 cm; (4) individuals > 75 g; (5) individuals 1+, average length: 11.8 cm

Study number	1a	1b	2	3	4	5	6	7
Sources	Frost (1939)		Swynnerton (1940)	Hartley (1948)	Frost (1950)	Nilsson (1957)	Ball (1961)	Horton (1961)
Country	IRELAND		G B	G B	G B	SWEDEN	G B	G B
Sites (lake/river)	r. Ballysmuttan	r. Strafian	l. Haweswater	r. Cam	r. Forss	r. Rensjöan	l. Llyn Tegid	r. Walla Brook
Sampling dates	I-XII	I-XII	V II		VI-VII	XIII (55)	I-XII (53)	I-XII (55-58)
Nb stomachs examined	219	340	92 (1)	30	74(2)	138	253	330
Nb of full stomachs	219	340*	92*	30*	74*	112	253*	330*

Study number	8	9a	9b	10	11	12a	12b	13	14	15
Sources	Thomas (1962)	Thomas (1964)		Maitland (1965)	Straskraba(1966)	Mann(1969)		Andreasson (1971)	Hunt (1972)	Pedley (1978)
Country	G B	G B		G B	CZECHOSLOVAKIA	G B		NORWAY	G B	G B
Sites (lake/river)	r. Teify	r. Rheidol	r. Pysgotwr	r. Endrick	r. Moravska	r. Bere	r. Docken	r. Trydea	l. Llyn Alaw	l. Llyn Dwythwch
Sampling dates	I-XII	II-V/XI-XII	I-II/VI-VIII	I-XII 61)	VII (62)	I- XII			I-XII (69-70)	I-XII
Nb stomachs examined	741	231	278	458	168 (3)	164 (4)	230 (4)	308 (5)	274	223 (1)
Nb of full stomachs	741*	231*	278*	458*	168*	164*	230*	308*	274*	223*

* Authors did not mention the number of empty stomachs

Study number	1a	1b	2	3	4	6	7	10	11	12a	12b	13	14	15	5	7	14	15	8	9a	9b	12
Methods	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% Vol.	% Vol.	% Vol.	% Vol.	% Points	% Points	% Points	% Weight
Chironomids (l/p)	16.7	11.4	18.2		11.2	20.7	8.7	20	5.5	2.5	7.5	27.1	1.4	32.8	4.6	8.8	0.2	4.2	1	12	5.3	
Simuliids (l/p)	7.8	11		0.7	0.1			4	11.6	7.5	4	2.7			1.8				0.5			
other Dipterans (l/p)	4.9	5.9			0.5							0.8										
Ephemeropterans (l/p)	12	10.8	29.7	6.3	21.5	2.7	8.4	11	10.4	4	4	13.9		8.5	2.1	8.1		3.6	6	10.8	5.3	4.2
Trichopterans (l/p)	10.3	9.6	7.3	21	18.7	10.3	24.5	2	38.8	32.5	20	9.4	0.2	16.1	21.6	15.4		32.2	63.6	34.6	38.6	31.3
Plecopterans (l/p)	25.7				0.2	2.3	15.4	5	2		10	6.3			3.1	1.6			5.9	25.3	13.3	1
Coleopterans (l/a)	1.7		14.9	26.5	24.7	0.2	2.4	2	2.5						8.3					1.2	1.6	
Megalopterans (l/p)				1		0.4						0.6			2.2	0.7			1.2			
Heteropterans (a)	2.2	1.8		2.2	0.2	0.2	2						11	3.8		0.4	13.1	8.7	2			
Terrestrial insects (a)	18.6	49.4	1.3	26.5	7.8	20.1	17.7	45	10.5	15	15	21.5		7.3	39.2	23.2		2.3	12.4	10.7	33.3	31.3
Total insects	**99.9**	**99.9**	**71.4**	**84.2**	**84.9**	**56.7**	**79.1**	**89**	**76.3**	**61.5**	**60.5**	**82.3**	**12.6**	**68.5**	**82.9**	**58.2**	**13.3**	**52**	**92.6**	**94.6**	**97.4**	**67.8**
Decapods		0.1		0.7																		
Amphipods			1	6	0.1	26		4	10.6	10	37.5	12.8	45.2			23.5	41.8		2.5	1.5		18.6
Isopods				0.2		5.3			5.3	2	1		36.7			4.3	10.2		1.2	1.1		
Cladocerans			1.4			4.1								9.1	5.6			0.1				
Copepods															1.9							
Total crustaceans		0.1	2.4	6.9	0.1	35.4	0	4	15.9	12	38.5	12.8	81.9	9.1	7.5	27.8	52	0.1	2.3			
Algae			1.6																			
Macrophytes			5																			
Total plants			6.6																			
Teleosts			2.2	1		0.1			0.3			2.5	0.8	3.3	2.8	12.1	18.5	39.2	5			
Fish eggs						5.1										1.7						
Molluscs			14.8	11.3	1.4	0.2				13.5	2	1.9	0.3	19.3	6.2		2	9.7	1			
Oligochets				0.2																		
Hirudineans													1.3				6		2			

(l/p) larvae and/or pupae; (l/a) larvae and/or adults; (a) adults; (l) larvae

(1) individuals > 15 cm (2) average length of individuals: 12.6 cm; (3) average length of individuals: 17.3 cm; (4) individuals > 10 cm; (5) individuals > 20 cm

October. It was thus proved that trout, and especially large specimens (Frost, 1939), favour surface feeding even if benthic organisms are in abundance (Ball, 1961; Dunn, 1952). Aerial surface prey consist essentially of dipterans, hymenopterans, trichopterans or plecopterans (Pentelow, 1932). The terrestrial insects are mainly coleopterans which have dropped from the banks or trees. The abundance of these organisms is closely linked to the richness of the riparian zone (Thomas, 1962; Egglishaw, 1967).

Trout feeds at the surface of relatively calm and slow running waters. It is easier for them to locate their prey in these sectors than in areas with turbulent currents (Egglishaw, 1967).

Of benthic insect larvae, the trout undoubtably prefers trichopterans. Trichopteran larvae are ingested throughout the year (Nilsson, 1957; Thomas, 1962; Sinha and Jones, 1967) sometimes in larger quantities during winter (Frost, 1939; Ball, 1961) and are often the main food source in both rivers and lakes (Hartley, 1948; Nilsson, 1955; Ball, 1961; Thomas, 1962; Straskrabra, 1965; Mann and Orr, 1969; Pedley and Jones, 1978). Ephemeropteran larvae are also common and average 10% of the trout's diet with the higher percentage for younger individuals (Straskrabra,1965; Neveu and Thibault, 1977). Plecopteran larvae, characteristically associated with headwater areas are highly predated by trout (Horton, 1961; Maitland, 1965; Crisp, 1983), especially in summer but quantitively represent only rather low proportions (Sinha and Jones, 1967; Frost, 1939).

All year classes of river and lake trout are curiously indiscriminate concerning predation of chironomids (Maitland, 1965). These prey items do not however constitute a large part of the trout's diet except when they are abundant (Valente and Heland, 1990).

In general, lake trout feeds less on insect larvae than river trout but the relative proportions of each taxon present in stomach contents are similar for both environments. The most sought-after prey of lake trout are trichopterans (Nilsson, 1955; Ball, 1961; Hunt and Jones, 1972). Lake trout feeds on isopods and amphipods mainly during winter and the beginning of summer (Ball, 1961; Maitland, 1965; Hunt and Jones, 1972). Molluscs, which are abundant in this type of environment, are ingested in larger and larger quantities as the fish grows (Allen, 1938; Swynnerton and Worthington, 1940; Nilsson, 1955; Hunt and Jones, 1972).

Trout can feed on fish eggs (Ball, 1962) and sometimes even on their own eggs (Egglishaw, 1967). This behaviour is usually associated with young specimens (< 90 mm). Nevertheless, during the spawning period, Thomas (1962) counted an average of up to 175 trout eggs in stomach contents of specimens of over two years of age.

Individuals of over 35 cm in size feed mainly on fish (Allen, 1938; Frost, 1939; Swynnerton and Worthington, 1940; Nilsson, 1955; Ball, 1962; Thomas, 1962). Nevertheless, in the main, Allen (1938), Frost (1939), Straskraba (1965), and Egglishaw (1967) all agree that the trout is not highly piscivorous.

Of high sport fishing value, the trout was often studied to estimate the degree of competition experienced in relation to coexisting species such as the bullhead (Muller, 1952; Straskraba, 1965; Brocksen *et al.*, 1968; Andreasson, 1971; Crisp, 1983), the minnow (Frost, 1939; Maitland, 1965; Straskabra, 1965; Lien, 1981), the eel (Thomas, 1962; Sinha and Jones, 1967; Mann and Blackburn, 1991). In the majority of cases, some trophic convergences, either seasonal or linked to different age groups, have been identified but in general, it is maintained that adult trout exploit their own ecological niche with their own distinctive feeding patterns. Interspecific competition to the detriment of trout has often been overestimated in previous research. The most active trophic concurrence clearly observed is that of young trout and smolt (Hartley, 1947; Frost, 1950; Thomas, 1962; Maitland, 1965).

The roach (*Rutilus rutilus* L.) (Table IV)

The roach is omnivorous but with high capacities for adaptation. It can survive on very little food (Brabrand, 1985) and exploits whatever food resource is available. Its diet is made up essentially of aquatic plants, molluscs, plankton, and to a lesser extent aquatic insects. Unlike the majority of other fish, the roach can live exclusively on one of these groups of food.

The roach exploits principally those food resources which are the most abundant. This ethological factor generally explains the correlation between the difference in proportions of food found in the stomach and those present in the environment.

Most work concerning the feeding behaviour of the roach acknowledges the preponderance of aquatic plant food in the diet of this species. In eutrophic lakes, for example, where roach have adapted and developed well (Niederholzer and Hofer, 1980; Brabrand, 1985), this type of food is very important and constitutes 80 or 90% of the diet (Prejs and Jackowska, 1978; Brabrand, 1985). This feeding strategy is not only due to the presence of a large aquatic plant mass in the environment but is also associated with a lack of, or, high competition for animal prey (Mann, 1965; Lyagina, 1972; Persson, 1983a; Vollestad, 1985; Brabrand, 1985). This strategy not only allows the roach to increase its competitiveness and biomass but also encourages the eutrophisation process and actually increases recycling of the aquatic plant mass and the liberation of nutrients immediately assimilated by plants (Brabrand, 1985).

As with all its food, the roach is not selective concerning the species of plant on which it feeds (Radforth, 1940; Brabrand, 1985). Consumption of macrophytes increases noticeably with age (Hartley, 1947; Holsik, 1967; Prejs and Jackowska, 1978; Brabrand, 1985) but decreases in oldest specimens (> 10 years) (Hellawell, 1972). Large quantities of diatoms are sometimes ingested (Radforth, 1940; Paschalski, 1958; Skora, 1964a). As much as 43% of nutrient volume can be made up of these organisms (Hellawell, 1972). Filamentous algae complete this aquatic plant type of feeding and occasionally become the principal food source, especially in summer when they are abundant (Hellawell, 1972; Persson, 1983a). Aquatic plant resources, exploited from May to October (Prejs, 1978; Niederholzer and Hofer, 1980; Persson, 1983a; Brabrand, 1965), are of low energetic value and limit growth. However they assure complementary food and sustain energy during unfavourable conditions (Gerdeaux, 1986).

Together with the bream (*Abramis brama* L.) and the tench (*Tinca tinca* L.), the roach ingests the largest quantities of zooplankton on reaching maturity. Although it is largely benthic, it can also feeds in midwater and even exclusively on pelagic prey (Roth, 1969; Brenner, 1973; Ponton and Gerdeaux, 1988). In certain environments (lakes), extremely high levels of zooplankton, of up to 42% of total weight of ingested food (Skora, 1964a), have been observed in roach stomach contents, whereas in other environments (midsized rivers), zooplankton is completely absent from the roach's diet (Paschalski, 1958; Hellawell, 1972; Mann, 1973; Tugarina, 1974; Brabrand, 1985).

Molluscs remain, however, the roach's main zoobenthic source of food. This food resource is especially exploited by individuals of > 150 mm and older fish (Hartley, 1947; Skora, 1964a; Roth, 1969; Prejs, 1976). When molluscs are abundant they can become the principal component of the roach's diet throughout the year. Tugarina (1974) and Rask (1989) observed populations where 68 to 98% of diet was made up of molluscs.

Table IV a, b. - Feeding habits of the adult roach (*Rutilus rutilus* L.), expressed as percentage occurrence, percentage number, percentage volume, percentage weight and percentage point.

Study number	1	2	3	4	5a	5b	6
Sources	Hartley (1948)	Hynes (1950)	Plisjka (1953)	Paschalski (1958)	Shora (1964)		Hellawell (1972)
Countries	G B	G B	POLAND	POLAND	POLAND		G B
Sites (lake/river)	r. Cam	r. Birket	l. Harsz	l. Roznow	l. Goczahowice	l. Kozlowa	r. Lugg
Sampling dates	I-XII (39-41)	I- XII	II-XII (49-51)	VII-IX (48)	IV-X (59-61)	V-IX (59-60)	I-XII (64-65)
Nb stomachs examined	166	236(1)	176 (2)	25	240 (3)	100 (4)	399
Nb of full stomachs	166*	163	176*	25*	240*	100*	399*

Study number	7	8	9	10	11
Sources	Prejs (1973)	Tugarina (1974)	Gerdeaux (1986)	Ponton (1988)	Rask (1989)
Countries	POLAND	C.I.S.	FRANCE	FRANCE	FINLAND
Sites (lake/river)	l. Warniak	l. Gusinoye	l. de Créteil	l. Léman	l. Tvärminne
Sampling dates	IV-XI (67-69)	V-X (64-67)	II-XII (80-81)	II-XII (84-85)	V-X (1975)
Nb stomachs examined	50	616	348(5)	389	372
Nb of full stomachs	50	616*	289	279	289

* Authors did not mention the number of empty stomachs

Study number	1	2	3	4	5a	5b	7	8	9	10	11	6 (6)
Methods	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.
Chironomids (l/p)	14.5	7.2	11.9	4.5	57.2	89	30		55*		9	1.4
Simuliids (l/p)	6											7.7
other Dipterans (l/p)	3				5.6	15	5					0.3
Ephemeropterans (l/p)	2						14	10				0.6
Trichopterans (l/p)	3.6*		3.7		28.2	91	25	17.5			1.7	10
Plecopterans (l/p)					11.6	2						
Coleopterans (l/a)	3.5				19.2	26						2.3
Odonatans (l)			1.5		18.1	37	2					
Heteropterans (a)		1.4			18.1	10						
Terrestrial insects		7.2					5					
Total Insects	39.8	14.6*	16.1*	4.5	100*	93*	61.9*	25*	55*		10.4*	26.3
Amphipods	8.4	5.8		4.5				22.5			2.9	0.3
Isopods			40.5								2.4	
Cladocerans			15.5		100	100*	18		41.5*	100		
Copepods	1.2				72.5*	50.3*	14		21.7	100		
Ostracods		4.3			52.9	60	10				2.9	
Total crustaceans	7.8	9.6*	48.5*	4.5	100	100*			52.4*	100	7.7*	0.3
Diatoms	7.2		2.9	86	100*	100*						13.4
Algae		11.6		27	97*	100*	96	25	32.3		3.5	21.4
Macrophytes	33.1	34.7	50.6	82.5	98.3*	100*	100	60.5	31		4	2.6
Total plants	37.4*	43.1*	51.8*	92.2*	100	100*	100	68.1	50.9		7	37.4
Teleosts												
Hydra					14.8	11						
Molluscs	21.1	23.2	53.1		89.5*	100*	8	75	6.5		100*	13.8
Oligochets							20		10			
Detritus		21		59								
Minerals		9										

(l/p) larvae and/or pupae; (l/a) larvae and/or adults; (a) adults; (l) larvae

*approximated % of occurrence

(1) 6 cm < individuals < 17 cm; (2) 8 cm < individuals < 32 cm; (3) 2 < year classes < 10; (4) 4 < year classes < 12; (5) year classes > 11; (6) data expressed in % of total occurrence

Study number	1	2	3	4	5	6a	6b	7	8a	8b	9	10
Sources	Hartley (1948)	Plisjka (1953)	Hellawell (1972)	Mann (1973)	Tugarina (1974)	Niederholzer (1980)		Persson (1983)	Vollestad (1985)		Brabrand (1985)	Rask (1989)
Countries	G B	POLAND	G B	G B	C.I.S.	AUSTRIA		SWEDEN	NORWAY		NORWAY	FINLAND
Sites (lake/river)	r. Cam	l. Harsz	r. Lugg	r. Stour	l. Gusinoye	l. Lanser	l. Möserer	l. Sövdeborg	l. Bjorkelangen	l. Rodenes	l. Oyeren	l. Tvårminne
Sampling dates	I-XII (39-41)	V-XII	I-XII (64-65)	I- XII	V-X (64-67)	IV-XII (76-77)		IV- XI	VI- X		V-XI (74-75)	V-X (1975)
Nb stomachs examined	166	176(1)	399	3 47	6 16	277	250	(2	2492	3095	861	372
Nb of full stomachs	166*	176*	399*	2 22	6 16*	277*	250*		2492*	3095*	861*	289

* Authors did not mention the number of empty stomachs

Study number	1	4	10	3	8a	8b	2	5	6a	6b	7	9
Methods	% Num.	% Num.	% Num.	% Vol.	% Vol.	% Vol.	% Weight	% Weight	% Weight	% Weight	% Weight	% Weight
Chironomids (l/p)	16.3	21.9	1.8	0.1			1.7				8.3	0.9
Simuliids (l/p)	20.7	10.7		2.4								
other Dipterans (l/p)	4.9			0.1								
Ephemeropterans (l/p)	6.3	10.2						2				
Trichopterans (l/p)	3.3	29.1	0.5	7.6			0.9	2.5			0.7	31.1
Coleopterans (l/a)	2.4			0.4								
Heteropterans (a)					3.6							
Terrestrial insects					3.6				1.1	4.8		
Total Insects	**56.4**	**71.9**	**2.3**	**11.1**	**8.5**	**1.4**	**2.6**	**4.5**	**5.5**	**4.8**	**13.5**	**35.6**
Amphipods	9.3				5.5	3.7		7.5				
Isopods					1.1		16.6					
Cladocerans					29.4	32.2	7.9		12	0.4	5.2	1.2
Copepods	2.2								11		3.8	
Ostracods			1.1									
Total crustaceans	**11.5**	**0.9**	**2**		**36**	**35.9**	**24.5**	**7.5**	**23**	**0.4**	**9**	**2.3**
Diatoms				42.6	19	17	2.9					
Algae				14.8	5	7			4.6	12.9	77 (3)	10
Macrophytes				3.1	6	10	29.3		20.5	6.6		25.7
Total plants				**60.5**	**30**	**37**	**32.2**	**20**	**25.4**	**19.5**	**77**	**35.7**
Teleosts					4.1							
Molluscs	29.1	18.4	96	20.8			37.8	68			0.2	8.6
Oligochets												
Detritus				7.8	19.6	20.3			40	73.6		5

(l/p) larvae and/or pupae; (l/a) larvae and/or adults; (a) adults; (l) larvae

(1) 8 cm < individuals < 32 cm; (2) individuals > 3 years; (3) algae + detritus

As a rule, aquatic insects and amphipodae rarely form part of the roach's diet. Only chironomid and trichopteran larvae are found consistantly in the stomachs.

Detritus is often present in roach stomachs (Paschalski, 1958; Niederholzer and Hofer, 1980; Vollestad, 1985). It is ingested especially in spring and winter and when there is a shortage of other foods (Radforth, 1940; Goldspink and Goodwin, 1979; Richeux *et al.*, 1992).

A few cases of piscivorous roach have been observed (Brabrand, 1985; Vollestad, 1985) but these remain marginal.

Finally, temperature appears to be an influential factor in the choice of food (Niederholzer and Hofer, 1980). Detritus are ingested at temperatures between 5 and 15°C and plants at between 15 and 20°C. At extreme temperatures of < 5 and > 20°C roach ingests more animal prey (Hellawell, 1972; Mann, 1973).

The dace (*Leuciscus leuciscus* L.) (Table V)

The dace is omnivorous and feeds essentially on aquatic insects and aquatic plants (Hartley, 1948; Healy, 1956; Hellawell, 1974). Its feeding rhythm, unlike many other fish, does not seem to be influenced by temperature (Hellawell, 1974) and seasonal trophic variations, except for winter and summer are relatively little marked (Hartley, 1947; Cragg-Hine, 1964a; Hellawell, 1974).

Table V. - Feeding habits of the adult dace (*Leuciscus leuciscus* L.), expressed as percentage occurrence, percentage number and percentage volume.

Study number	1	2a	2b	3	4
Sources	Hartley (1948)	Hellawell (1974)		Mann (1973)	Clavel (1977)
Countries	G B	G B		G B	FRANCE
Sites (lake/river)	r. Cam	r. Afon Llynfi	r. Lugg	r. Stour	r. Loire
Sampling dates		I-XII (64)		I-XII	IV (76)
Nb stomachs examined	23 1	40 9	36 6	507	
Nb of full stomachs	23 1*	40 9*	36 6*	407	

* Authors did not mention the number of empty stomachs

Study number	1	2a	2b	1	3	4	2a	2b
Methods	% Occ.	% Occ.(1)	% Occ.(1)	% Num.	% Num.	% Num.	% Vol.	% Vol.
Chironomids (l/p)	12.1	18.1	10.4	14.6	13.6	58.6	7.1	4
Simuliids (l/p)	8.2	3.5	15.2	13.9	14	3.1	0.9	16.7
Ephemeropterans (l/p)	4.5*	6.2	1.9	9.3	13.8	1.9	3.5	1.6
Trichopterans (l/p)	30	11	17.6	23.6	39.8	17.5	17.8	15.4
Plecopterans (l/p)		5.4	4.4				2	0.6
Coleopterans (l/a)	8	3.8	4.9	4.9			0.8	1.7
Terrestrial insects	1.6*	9.5	12.2	5.1	1.8		8.1	14.5
Total insects	**58.4**	**53.6**	**59.8**	**71.4**	**81.2**	**93.6**	**35.1**	**54.4**
Amphipods	5.3	2.2	2.2	10	0.1		2	2
Isopods	0.4	0.3						
Molluscs	9.5	1.2	10.8	16.1	2.5		1.4	8.1
Oligochets		0.2						
Diatoms	11.7							
Algae	9	15.2	8.2				36.6	17
Macrophytes	3	0.2	1.6					
Detritus		14.9	4.3				15.7	3

(l/p) larvae and/or pupae; (l/a) larvae and/or adults; (a) adults; (l) larvae

*approximated % of occurrence

(1) data expressed in % of total occurrences

Among prey of animal origin, trichopterans and molluscs, depending on their abundance, make up the principal mass of the dace's diet. Trichopterans are ingested mainly in winter and spring (Hartley, 1947; Cragg-Hine, 1964b; Hellawell, 1974; Mann, 1974) whereas molluscs become present in the diet of dace during the second half of the year (Hartley, 1947; Cragg-Hine, 1964b). Quantitatively, dipteran larvae represent a large proportion of the prey of dace (Clavel *et al.*, 1977), especially in summer (Mann, 1974) but their contribution in weight is low.

Oligochaets, in spite of their absence from stomach contents in the majority of studies, are an important source of food. In fact 3 hours after their ingestion, they are almost entirely digested and after 24 hours the presence of oligochaets can only be detected by observing the parasites in the stomach contents (Kennedy 1969). Kennedy (1969) noticed very high predation of oligochaets during winter and spring; oligochaets had been ingested by up to 60% of fish observed during this period.

The dace feeds regularly on allochtonous insects, especially in summer (Cragg-Hine, 1964b), but this decreases with age (Hellawell, 1974).

On the contrary, ingestion of aquatic plant matter, especially filamentous algae increases with size (Hartley, 1948; Hellawell, 1974). This source of nutrition is relatively important and makes up, on average, nearly a quarter of the volume of stomach contents of fish caught by Hellawell (1974). Macrophytes can occasionally become the main source of aquatic plant nutrition for adults (Mann, 1974) whereas diatoms, that of fingerlings. The dace does not often predate other fish but ingests detritus all year round (Hellawell, 1974).

The chub (*Leuciscus cephalus* L.) (Table VI)

The chub is one of the rare species of omnivorous fish where the adult's diet is made up of fish and aquatic plant matter in equal proportions.

The principal source of nutrition, however, remains aquatic plant matter and this comprises on average nearly half its food and even more than half in summer (Hellawell, 1971; Mann, 1976; Adamek and Obrdlik, 1977). Hellawell (1971) even compares the chub's feeding behaviour to that of herbivorous species. The few studies made on stomach contents reveal a preference for macrophytes, especially for adults (Gyurko and Nagy, 1965; Leeming, 1967; Hellawell, 1971). During its growing period the chub's ingestion of aquatic plant matter increases astonishingly (Leeming, 1967; Mann, 1976); only the oldest specimens (+9) progressively decrease exploitation of this resource (Hellawell, 1971).

Principal animal prey are fish (Hellawell, 1971; Mann, 1976). Ingestion increases in winter (Hellawell, 1971) and naturally with the age of the fish (Crag-Hine, 1964; Hellawell 1971; Mann, 1976). However, according to observations, the chub is not the source of fingerling devastation as commonly put forward (Crag-Hine, 1964; Hellawell 1971; Mann, 1976).

Of insect larvae, trichopterans are without doubt the most sought after prey group (Hellawell, 1971; Mann, 1976; Adamek and Obrdlik, 1977) and make up a large percentage of the winter and spring diet. Depending on the case, they are mainly ingested by young fish (Hellawell, 1971) or adult fish (Mann, 1976). Because of their size, chironomids are the principal food source of young fish (Mann, 1976). The chub readily ingests flying insects and predates crayfish without hesitation when they are present (Hellawell, 1971; Mann, 1976).

Detritus is a relatively important source of food for this species (Hellawell, 1971) and even comprised the major part of the nutritive mass of the fish which were examined by Adamek and Obrdlik (1977).

Table VI. - Feeding habits of the adult chub (*Leuciscus cephalus* L.), expressed as percentage occurrence, percentage number, percentage volume and percentage weight.

Study number	**1a**	**1b**	**2**	**3**
Sources	Hellawell (1971)		Mann (1976)	Adamek (1977)
Countries	G B		G B	CZECHOSLOVAKIA
Sites (lake/river)	r. Lugg	r. Afon Llynfi	r. Stour	r. Oslava
Sampling dates	I-XII (64-65)			I-XII (72-75)
Nb stomachs examined	62 6	27 8	8 7 (1)	12 3
Nb of full stomachs	41 6	24 8	6 1	12 3*

* Authors did not mention the number of empty stomachs

Study number	**1a (2)**	**1b (2)**	**2**	**3**	**2**	**1a**	**1b**	**3**
Methods	**% Occ.**	**% Occ.**	**% Occ.**	**% Occ.**	**% Num.**	**% Vol.**	**% Vol.**	**% Weight**
Chironomids (l/p)	0.7	3.1			8.7			
Simuliids (l/p)	2.5					0.4		
Trichopterans (l/p)	14.6	13.5			13	7	9.9	3.8
Plecopterans (l/p)	2	3.8				0.2	0.4	
Coleopterans (l/a)					6.5			
Terrestrial insects	10.7	10.3			4.3	2.5	1.9	
Total insects	**24.6**	**25.4**	**30.7**	**28.7**	**32.5**	**11.5**	**10.4**	**4.5**
Diatoms	7.4	13.1		20.9		7.2	28.1	16.1
Algae	18.4	18.1	10.7	22.1		21.1	39.4	15.3
Macrophytes	11.2	9.2	37.5	27.8		14.6	7	19.8
Total plants	**37**	**40.4**				**42.9**	**74.5**	**51.2**
Decapods					8.8			
Amphipods					4.3			
Teleosts	14.1	8.1	7.1	3.9	34.8	28.6	8.1	2.1
Ducks					2.2			
Detritus	9.4	13.1		52.7		4.8	2.4	38.1

(l/p) larvae and/or pupae; (l/a) larvae and/or adults; (a) adults; (l) larvae

(1) individuals > 15 cm; (2) data expressed in % of total occurrences

The minnow (*Phoxinus phoxinus* L.) (Table VII)

The minnow, together with the roach and the dace is classed in the group of vegeto-insectivorous fish (Hartley, 1948). It is actually one of the few headwater fish which feeds on diatoms and filamentous algae. On average more than 40% of minnows regularly feed on aquatic plant matter (Geyer and Mann, 1940; Tack, 1940; Frost, 1943; Hartley, 1948; Maitland, 1965) and generally all through the year (Frost, 1943). Filamentous algae can even become the principal source of food (Straskraba *et al.*, 1966). Aquatic plant matter is ingested mainly by adults of over one year (Frost, 1943).

Chironomids are the main food source for river minnow and make up, on average, a third of their diet (Tack, 1940; Frost, 1943; Hartley, 1948; Maitland, 1965; Straskraba *et al.*, 1966). On the contrary, lake fish feed on less chironomids (< 10% of diet) in spite of their relative abundance in the environment (Frost, 1943; Myllylä *et al.*, 1983). According to studies, consumption varies with age group. Frost (1943) observed that few dipterans were eaten by adults (less that 12% of diet for specimens > 60 mm), whereas for Straskraba *et al.* (1966) chironomids represented 89% of the diet of 3+.

Minnow appear to avoid plecopterans and trichopterans (Frost, 1943; Hartley, 1948; Maitland, 1965; Straskraba *et al.*, 1966; Lien, 1981) which only make up respectively 1% and 3% of their diet. Trichopterans are ingested in winter and mainly by adults (Frost, 1943; Mann and Orr, 1969) whereas ephemeropterans, which are more sought after (> 10% of river fish diet) are ingested in summer. In certain circumstances, aerial insects make up a significant part of the minnow's diet (Tack, 1940; Frost, 1943; Maitland, 1965).

Table VII. - Feeding habits of the adult minnow (*Phoxinus phoxinus* L.), expressed as percentage occurrence and percentage number.

Study number	1	2a	2b	3	4	5	6	7	8	9
Sources	Tack (1940)	Frost (1943)		Hartley (1948)	Maitland (1965)	Straskraba (1966)	Mann (1969)	Neveu (1981b)	Lien (1981)	Myllylä (1983)
Countries	GERMANY	G B		G B	G B	CZECHOSLOVAKIA	GB	FRANCE	NORWAY	FINLAND
Sites (lake/river)	r.?	r. Brathay	l. Windermere	r. Cam	r. Endrick	r. Moravska	r. Bere	r. La Nivelle	l. Heimdalsvatn	l. Papulampi
Sampling dates		I-XII (40-41)		I-XII (39-41)	I-XII 61)	VII (62)	I-XII	VI (76)	VI-X (75-77)	
Nb stomachs examined	472 (1)	833	1228	12 6	37 0	79	369	97 (2)	654	1 99
Nb of full stomachs	472*	833*	1228*	12 6*	37 0*	79*	369*	44	654*	1 89

* Authors did not mention the number of empty stomachs

Study number	1	3	4	8	2a	2b	3	4	5	6	7	8	9
Methods	% Occ.	% Occ.	% Occ.	% Occ.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.
Chironomids (l/p)	46.2	26.5	60.3*	48.8	20.1	8.8	67.4	36	85.2	18.8	37.5	19.5	2.8
Simuliids (l/p)	2.5	1.6	15.6*								15.1		
other Dipterans (l/p)	8	4.8	23.2*				4.3	14.5	4.4	21			
Ephemeropterans (l/p)	8.9	3.2*	37.7*		11.9	6.1	3.3	11	7	18.2	24.6	0.9	
Trichopterans (l/p)	19.9	1.6	8*	8.4	9.3	6.1	1.6	2	0.1	7.1	15.1	0.3	
Plecopterans (l/p)	4.9		13.8*		1.6	1		3				0.4	
Coleopterans (l/a)	4.7	1.6	27.6*				1.6	14	2				
Odonatans (l)	0.6												
Terrestrial insects	20.1	3.2	32.8*		6.5	7	3.8	10			7.6		
Total insects	**78.8***	**51.6**	**100***	**50.3***	**51.8**	**29.7**	**83.7**	**90.5**	**98.7**	**65.1**	**100**	**21.1**	**3**
Decapods		3.2											
Amphipods	0.8	4	12	3.2	0.7	1.8	2.7	3		7.2		0.7	
Copepods	14	1.6			0.6	11.3	3.2						0.3
Cladocerans	23.5	1.6		87.2	1.9	21.3	4.3					77.6	95.6
Ostracods	2.5												
Total crustaceans	**35.4***	**11.1**	**12**	**87.3***	**3.2**	**34.4**	**10.2**	**3**		**7.2**		**78.3**	**95.9**
Diatoms	41.1	27			8.5	9.9							
Algae	48.2*	25.4	28	13.5	23	11.8							
Macrophytes	26.5*												
Total plants	**78.5***	**43.8**	**28**	**13.5**	**31.5**	**21.7**							
Teleosts	2.3												
Fish eggs				8.8									
Molluscs	7.4*		3*	13.6	0.6	2.4		2		4.2			0.1
Oligochets	11.6*		7*		1	0.5		3					
Detritus	49.4				7.1	5.9							

(l/p) larvae and/or pupae; (l/a) larvae and/or adults; (a) adults; (l) larvae

*approximated % of occurrence

(1) Phoxinus laevis; (2) 3.8 cm < individuals < 8.6 cm

Cladocerans are the principal food source in lakes, especially for the younger minnow (Frost, 1943; Lien, 1981). They are ingested from May to October and sometimes in even larger quantities in autumn (Myllylä *et al.*, 1983), whereas copepods are present mainly in the first half of the year (Frost, 1943).

Myllylä *et al.* (1983) found fish eggs in certain stomachs whereas it is more usual to find oligochaets and molluscs in winter (Maitland, 1965; Mann, 1986).

Older minnow and young trout have quite similar diets (Maitland, 1965; Frost, 1943; Lien, 1981), but the minnow's diet is more varied and this allows it to withstand competition.

The gudgeon (*Gobio gobio* L.) (Table VIII)

The gudgeon is a benthic insectivorous fish (Bernet, 1960; Brunet and Hoestlandt, 1972) which, depending on its environment, diversifies its feeding behaviour by ingesting molluscs, plankton or aquatic plant matter. It feeds throughout the year (Neveu, 1981b), but in an irregular manner. Hartley (1948), Bernet (1960) and Brunet and Hoestlandt (1972) observed that almost 33% of fish sampled had empty stomach contents.

Insect larvae make up more than 66% of the gudgeon's diet. These are ingested mostly at the end of spring. In the study made by Bernet (1960), they represented even up to 97% of the total quantity of ingested prey during this period. The majority of these insects are chironomids and are the gudgeon's principal source of food, in common with most benthic fish (Hartley, 1948; Bernet, 1960; Kennedy and Fitzmaurice, 1972; Neveu, 1981a). After chironomids and ephemeropterans, trichopterans are the most popular choice of aquatic larvae. In June, trichoperans can make up 30% of diet (Bernet, 1960). In autumn and winter, once aquatic insects are no longer available, molluscs become the gudgeon's principal source of food, especially in rivers. From September to January, they constitute up to 90% of the gudgeon's diet (Bernet, 1960; Kennedy and Fitzmaurice, 1972).

Predation of zooplankton is low in rivers, but higher in lakes and by young fish. However, Kennedy and Fitzmaurice (1972) found cladocerans and copepods in 40% of specimens of over 7.5 cm.

The gudgeon often feeds on aquatic plant matter, especially filamentous algae (Radforth, 1940; Gyurko and Nagy, 1966; Brunet and Hoestlandt, 1972). These algae made up more than 35% of ingested food in the studies made by Gyurko and Nagy (1966) and by Kennedy and Fitzmaurice (1972).

Although the gudgeon is a benthic fish it ingests very few amphipods (less than 5%), and it only rarely feeds on other fish. Only Brunet and Hoestlandt (1972) reported presence of fish in the stomach contents of 2 gudgeons out of 75.

According to Hartley (1948), the gudgeon's feeding behaviour is very similar to that of the bullhead even though it does not have the same type of habitat.

The bream (*Abramis brama* L.) (Table IX)

The bream's diet, as with most other fish, changes as it grows. During the first three years of life the majority of its diet is made up by zooplanktonic forms of cladocerans and copepods and, to a lesser extent and in lower quantities, by chironomid larvae and molluscs (Hartley, 1947; Kennedy and Fitzmaurice, 1968; Tatrai 1980; Granado-Lorecia and Garcia-Novo, 1986; Lammens and Hoogenboezem, 1991).

During the adult phase of life, zooplankton continues to be exploited, without however increasing to more than 10% of the nutritive mass (Lammens, 1984), but the bream's diet becomes almost exclusively demersal and consists largely of chironomid larvae which constitute more than 66% of food ingested (Pliszka, 1953; Budzynska *et al.*, 1956; Prejs,

Table VIII. - Feeding habits of the adult gudgeon (*Gobio gobio* L.), expressed as percentage occurrence and percentage number.

Study number	1	2	3	4	5A	5B	5C	6	7	8
Sources	Stankovitch (1921)	Hartley (1948)	Bernet (1960)	Gyurko (1966)		Kennedy (1972)		Brunet (1972)	Neveu (1981b)	Chappaz (1988)
Countries	FRANCE	G B	FRANCE	RUMANIA		IRELAND		FRANCE	FRANCE	FRANCE
Sites (lake/river)		r. Cam	r. Nivelle		r. Sullane	l. Carrigadrohid	l. Inniscana	r. de la Mont. Noire	r. La Nivelle	l. Sainte-Croix
Sampling dates			I-IX (58-59)		X (69)	II (65)	V-VI (65-66)	I-VIII (70-71)	VI (76)	I/IV/V/IX
Nb stomachs examined	20	391	515 (1)	119 (2)	25 (3)	41 (4)	46 (5)	75 (6)	89 (7)	166 (8)
Nb of full stomachs	20*	391*	254	119*	25	38	34	75*	89*	166*

* Authors did not mention the number of empty stomachs

Study number	2	5A	5B	5C	1	2	3	4	6	7	8
Methods	% Occ.	% Occ.	% Occ.	% Occ.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.
Chironomids (l/p)	61	15	60	77		49.9	23.8			20.7	25
Simuliids (l/p)	9.2					11.9	17.3			33.9	5
other Dipterans (l/p)	9.5					5.1	0.7			0.4	4
Ephemeropterans (l/p)	8.2	20		14		5.3	9.8			32.2	6.1
Trichopterans (l/p)	6.1	12				1	10.1			1.1	13
Plecopterans (l/p)				8.5			0.2			0.7	
Coleopterans (l/a)	3.6		3			0.5				3.6	2
Megalopterans (l/p)	3.8					0.6					
Total insects	**71.8**	**39.6***	**60.9***	**80.3***	**65.1**	**74.3**	**61.9**	**50.5**	**78.1**	**92.6**	**55.1**
Amphipods	18.1					8.8	1.6			1.4	
Isopods	7.4	15	5	40		4.2					
Copepods	8.9		10	15		4.5					
Ostracods	3.8					1.6			9.8		11.4
Total crustaceans	**30.4**	**15**	**14.1***	**47.8***	**12.2**	**19.1**	**1.6**	**1.6**	**9.8**		**11.4**
Molluscs	15.3	90		6	15.1	5.9	33.8		5.6	5.7	22.8
Oligochets			10	5	3.7		0.04	9.7	3.7		6.6
Diatoms	0.5			14							
Algae	6.9	50	3	5				35.7			
Detritus		15	40	20							

(l/p) larvae and/or pupae; (l/a) larvae and/or adults; (a) adults; (l) larvae

*approximated % of occurrence

(1) individuals > 9 cm; (2) Gobio obtusirostris; (3) individuals > 9.5 cm; (4) (5) individuals > 7.5 cm; (6) average length: 11.2 cm; (7) 4.1 cm < individuals < 15.6 cm; (8) average lenght: 12.5 cm

Table IX. - Feeding habits of the adult carp (*Cyprinus carpio* L.), expressed as percentage occurrence and percentage weight.

Study number	**1**	**2**	**3**	**4**	**5**	**6**
Sources	Astanin (1967)	Popovska (1972)	Prejs (1973)	Tugarina (1974)	Guziur (1976)	Crivelli (1979)
Countries	**CIS**	**YUGOSLAVIA**	**POLAND**	**C.I.S.**	**POLAND**	**FRANCE**
Sites (lake/river)	l. Yegorlyk	l. Prespa	l. Warniak	l. Gusinoye	l. Klawoj	l. Camargue
Sampling dates	V-IX (62-65)	V-IX (67-70)	IV-XI (67-69)	V-X (64-67)	V-XI (69-70)	V-VIII
Nb stomachs examined	373	108	249	425 (1)	338	72
Nb of full stomachs	324	108	229	425*	269	43

* Authors did not mention the number of empty stomachs

Study number	**1**	**2**	**3**	**4**	**5**	**6**	**1**	**2**	**3**	**4**	**5**
Methods	**% Occ.**	**% Occ.**	**% Occ.**	**% Occ.**	**% Occ.**	**% Occ.**	**% Weight**	**% Weight**	**% Weight**	**% Weight**	**% Weight**
Chironomids (l/p)	61.6	71.3	97	78.7	90	62.8	10		25	32.7	23.9
other dipterans (l/p)			57.6*						8.5		
Ephemeropterans (l/p)			87	24.5	22.9	7			16	4.4	
Trichopterans (l/p)		7.4	92	35	52					4.5	8.4
Coleopterans (l/a)	10		16		16.7	60.5	2				1
Megalopterans (l/p)			16		34.2						7.5
Heteropterans (a)						14					
Odonatans (l)			57		21.5	4.6			5		
Terrestrial insects (a)			57								2.8
Total insects	**67.6***	**72.9***	**100***	**86.5***	**100***	**86**	**12**	**17.4**	**54.5**	**41.6**	**50**
Amphipods		26.8	2	11.3	1.1	18.6		11.6		0.6	
Isopods		11.1	10								
Cladocerans	14	23.1	84	44.3	35.6	46.5	1.4		8	2.5	
Copepods	14	17.6	75		32.7	48.8	1		4		
Ostracods		15.7	82		25.6	69.8			3		
Total crustaceans	**26.5***	**71.1***	**100***	**49.6***	**69.4***	**76.7**	**2.4**	**12**	**15**	**3.1**	
Diatoms		68.5									
Algae		12	90		22.5	30.2					
Macrophytes		13.9	94	87.5	85.5				14.7	29.7	6
Total plants	**62.1***	**74.8**	**100***	**87.5**	**86.5***	**30.2**	**17.8**	**1**	**15**	**29.7**	**6**
Teleosts			5								
Molluscs		60.1	65	90	83.1*	20.9		19.8	14	24.1	39.2
Oligochets	25	13.9	76		46.5		3.7	3.1			
Hirudineans			9								
Detritus	82.1	86.1				100	53.1	46.1			
Seeds			7		11	93					

(l/p) larvae and/or pupae, (l/a) larvae and/or adults, (a) adults, (l) larvae

*approximated % of occurrence

(1) Cyprinus carpio haematopterus, individuals > 2 ans

1973; Zadorozhnaya, 1977; Koslova and Panasenko, 1977). Therefore, along with the carp, the bream can be considered as the largest consumer of Chironomids (Neubaur, 1926).

The diet of older specimens is more varied and these fish can occasionally feed on odonatans (Solovov, 1970; Prejs, 1973), trichopterans (Kennedy and Fitzmaurice, 1968; Prejs, 1973) and amphipods (Kennedy and Fitzmaurice, 1968; Giles *et al.*, 1990). However in this age group, it is mainly oligochaets and molluscs which are ingested in large quantities (Pliszka, 1953; Budzynska *et al.*, 1956; Kennedy and Fitzmaurice, 1968; Solovov, 1970; Prejs, 1973; Tatrai, 1980).

Molluscs are sought after by bream of > 4 years of age (Budzynska *et al.*, 1956) and are found in almost 80% of specimens > 30 cm (Solovov, 1970).

In the same way oligochaets, when abundant (Zadorozhnaya, 1977), can make up the major part of the bream's diet reaching up to 22% of ingested prey (Kennedy and Fitzmaurice, 1968; Kennedy, 1969) especially in individuals of 6 years and over (Budzynska *et al.*, 1956).

Food from aquatic plant sources is eaten mostly by older fish, but in relatively small quantities and made up essentially of macrophytes and filamentous algae. The latter are probably ingested accidentally during the search for potential prey (Budzynska *et al.*, 1956; Zadorozhnaya, 1977).

The bream's food resource range varies significantly in lakes where animal plankton, in the form of cladocerans, copepods, and ostracods, represents a large proportion of the adult bream's prey (Budzynska *et al.*, 1956; Zadorozhnaya, 1977).

The carp (*Cyprinus carpio* L.) (Table X)

The carp is not exclusively herbivorous as was once thought. It is a mainly omnivorous species with strong carnivorous tendencies (Crivelli, 1981). Animal prey actually represents 75% to 95% of its diet (Prejs, 1973; Guziur, 1976; Tugarina, 1974). The carp exploits not only the most abundant resource (Wunder, 1938; Schaperclaus, 1962; Fanget, 1972; Uribe-Zamora, 1975) but it also selects prey of which it is physiologically most capable of capturing (Fanget, 1972; Stein *et al.*, 1975; Crivelli 1979). The size of prey is of course, an important factor in the choice of capture. The carp feeds mainly at the beginning and end of the day (Fanget, 1972) and very actively during the summer, as do many other fish. In winter, its feeding rhythm becomes perturbed at temperatures below 10°C (Popovska-Stankovic, 1972), and almost non-existant at below 6°C (Sibbing, 1988).

From spring to summer, zooplankton is an important food source (Wunder, 1938; Astanin, 1969; Guziur, 1976; Sibbing, 1988). It is ingested by all carp during this period, but nevertheless does not represent a large nutritional mass, generally less than 5%. Because of this, zooplankton is often considered to be a secondary or alternative source of food (Guziur, 1976; Grando-Lorencio and Garcia-Novo, 1986). However, Wunder (1938) observed 3-summer-old carp ingesting up to 600 g per day of cladocerans.

In spite of the high occurrence of aquatic plant matter, notably macrophytes, in stomach contents, these represent only a relatively small part of the carp's diet. Quite large quantities can be ingested (Fanget, 1972) when they become available in summer (Wunder, 1938; Guziur, 1976; Tugarina, 1974; Sibbing, 1988) but during the other seasons aquatic plant matter constitutes less than 10% of the carp's diet (Guziur, 1976; Tugarina, 1974). A high ingestion of aquatic plant matter is often a sign of deficiency in animal prey (Sibbing, 1988). The carp actually feeds more often on dead macrophytes and rarely on green ones (Paopovska-Stankovic, 1972; Fanget, 1972; Crivelli, 1981). These forms of detritus are

Table X. - Feeding habits of the adult bream (*Abramis brama* L.), expressed as percentage occurrence, percentage number and percentage weight.

Study number	1	2a	2b	3	4	5	6	7	8	9	10	11	12
Sources	Hartley (1947)	Laskar (1948)		Pliszka (1953)	Budzynska (1956)	Abdullayev (1965)	Kennedy (1968)	Solovov (1970)	Prejs (1973)	Zadorozhnaya (1977)	Koslova (1978)	Lammens (1984)	Giles (1990)
Countries	G B	GERMANY		POLAND	POLAND	C.I.S.	IRELAND	C.I.S.	POLAND	C.I.S.	C.I.S.	NORWAY	G B
Sites (lake/river)	l. Norfolk broads	l.Tiefen	l. Flachen	l. Harsz	l. Goplo	l. Kuyu-Mazar	l. Town,Castle,Main	r. Ob	l. Warniak	l. Mozhaysk	l. Courland	l. Tjeukemeer	l. Main & St Peters
Sampling dates	I-XII (39-40)			II-XII (49-51)	VII (49)			(66-69)	IV-XI (67-69)	V-XII (69-70)	I-XII (70-74)	VI-IX (79-82)	V-VII (86-87)
Nb stomachs examined	1239	1228	288	111 (1)	20 1(2)	38 (3)	137 (4)	44 (5)	5 6	1 94		6)	126
Nb of full stomachs	787	1228*	288*	111*	20 1*	2 4	9 8	44*	5 4	1 94*			126*

* Authors did not mention the number of empty stomachs

Study number	1	2a	2b	3	4	6	7	8	2a	2b	4	5	7	11	12	3	4	8	10	9
Methods	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% Weight	% Weight	% Weight	% Weight	% Weight
Chironomids (l/p)	20.1*	100*	51.2*	95.5*	100	44.9	90	96	49.5	24.2	15	47.2	78.9	25.6	61.9	56.9	72.9	63	87.5	91.5
other Dipterans (l/p)		13*	12.5	26.2	7			22								3.5	0.1			
Ephemeropterans (l/p)		8.1*	8.3	1.5	33	12.7	31	70	1.4	3.2	0.7		1.1		1.1		0.5	5.6		
Trichopterans (l/p)	0.5*	5.4*	19.3*		26.2*	30.7	16	85	1	8.1	0.8		0.5		1.1		6.5	9.3	0.1	
Plecopterans (l/p)					1															
Coleopterans (l/a)		0.3	1.7*		7															
Megalopterans (l/p)		0.8	3.1		2			5												
Heteropterans (a)	0.5					4.1									1.1					
Odonatans (l)					2		46	41				3.5	1.4				1.3	2.8		
Total insects	20.8*	100*	69.6*	96.5*	100	67.4	92*	100*	54.8	41.5	14.3	50.5	81.9	25.6	65.2	60.4*	74	79.7	88.5	94.7
Amphipods	0.5	0.5			8	21.6					0.02				3.9		1.7			
Isopods		2	2.8	12.7	43	10.8				1.1	0.3				3.8	6.9	0.4			
Cladocerans	44.6*	99.1*	57.3*	43.5	98*	20.7	16	59	26	28.1	50.2	20.8	5.5	64.1		9.4	5.8	4.7	7.7	0.6
Copepods	45.1	41.6*	31.2		79.3*	6.6	26	56	8.2	12.1	12.9	23.9	8.1	10.2			1.1		1.9	
Ostracods	4.1	19.5	6.9		44	1.9		68	3.4	2.6	1.7						0.2			
Total crustaceans	68.7*	100*	71.5*	49.7*	100*	50*	36.6*	95.6*	37.6	43.9	65.1	44.7	13.6	74.3	7.7	16.3*	7.5	4.7	9.8	0.6
Macrophytes	0.1	25.2	31.6		53			65	0.8	4.2								6.7		
Algae	0.1	9.6*	11.1		24.9*		31	73	5.9	8	5.9							0.3		0.6
Diatoms	0.6	28.2	14.2		33						2.3									
Total plants	0.8	50.6*	47*		75.7*		31	85.3*	6.7	12.2	8.2							7		0.6
Molluscs	0.2	4.2*	10*		24*	37.8	79	58		2.5	0.07		3.2		23.5		9.8	4.7	0.3	
Oligochets		31.4*	20.8	44.2	42			65		6.9	4.8					18.6	7.6			1.5

(l/p) larvae and/or pupae; (l/a) larvae and/or adults; (a) adults; (l) larvae

*approximated % of occurrence

(1) 11 cm < individuals < 40 cm; (2) 1+ < individuals < 11+; (3) Abramis brama bergi > 17 cm; (4) individuals > 28 cm; (5) individuals > 22 cm; (6) 15 cm < individuals < 25 cm

regularly ingested in winter and can represent 80% of the weight of food during this period (Popovska-Stankovic, 1972; Astanin, 1969).

Chironomids are recognized by all authors as being the carp's primary source of food. They are ingested by nearly 80% of fish examined and constitute about 25% of the total weight of their food. These benthic prey become present in the carp's diet at the end of spring (Guziur, 1976) and continue all through the summer until autumn (Tugarina, 197l; Fanget, 1972). Chironomid larvae live in organically rich beds, notably in aquatic plant debris with which they are often ingested (Wunder, 1938; Guziur, 1976). Wunder (1938) thus observed up to 4,000 larvae for one litre of aquatic plant matter in decomposition, which explains the high concentrations of these two types of food in stomach contents. Furthermore, the carp is one of the species which exploits benthic resources the most, in spite of low oxygen levels (Astanin, 1969).

Molluscs are the second category of prey most sought after by the carp. They are more often present in the stomach contents of adult specimens but constitute, like chironomids, on average 25% (Guziur, 1976) of the weight of ingested food. Molluscs are sometimes dominant in the carp's diet (Spet, 1961; Popovska-Stankovic, 1972; Guziur, 1976) especially in summer (Fanget, 1972) and autumn.

Other larvae like ephemeropteran or trichopteran larvae can be well represented in the carp's diet (Prejs, 1973; Guziur, 1976), or odonatan larvae (Prejs, 1973; Guziur, 1976; Crivelli, 1979) which are not often ingested by other fish.

Oligochaets are present in almost one third of stomach contents, especially in winter and at the beginning of spring (Sibbing, 1988) and make up a relatively important part of the carp's diet (Wunder, 1938; Astanin, l969; Prejs, 1973; Guziur, 1976).

Curiously the carp readily feeds on grain. Numerous authors have found grain in stomach contents (Wolny, 1962; Szumiec, 1963; Prejs, 1973; Guziur, 1976; Crivelli, 1981).

Examples of piscivorous carp are very rare and this phenomenon is generally caused by an abundance of fry in a relatively poor trophic context (Dyk, 1956; Prejs, 1973; Steffens, 1980).

The tench (*Tinca tinca* L.) (Table XI)

Of the wide variety of food which makes up the diet of the tench, animal prey is its principal source of nutrition. Chironomid larvae, trichopteran larvae and molluscs alone make up a major part of stomach contents, whereas aquatic plant matter makes up only a relatively small proportion of this species diet.

Zooplankton is the basic food of young specimens of less than 4 years in age (< 21 cm) (Kennedy and Fitzmaurice, 1970; O'Maoileidigh and Bracken, 1989) but is a source of food exploited by practically all adult tench (O'Maoileidigh and Bracken, 1989; Giles *et al.*, 1990) without however representing a large volume, except in a few cases (Giles *et al.*, 1990). Over 4 years of age, macroinvertebrates become the principal element of the tench's diet.

Chironomid larvae, which constitute on average 20% of the weight of food (Prejs, 1973), are found in nearly 75% of stomach contents. Trichopteran larvae and molluscs are also equally highly prized by tench, especially the adults (O'Maoileidigh and Bracken, 1989). These two types of prey represent about half the total nutritional mass for this age group (Prejs, 1973; Giles *et al.*, 1990) and sometimes even more (Skora, 1964b). Higher crustaceans and odonatan larvae can, depending on abundance in the environment, become a significant part the tench's diet (Pliszka, 1953; Prejs, 1973; Giles *et al.*, 1990; Kennedy and Fitzmaurice, 1970).

Table XI. - Feeding habits of the adult tench (*Tinca tinca* L.), expressed as percentage occurrence, percentage number, percentage volume and percentage weight.

Study number	1	2	3	4	5	6a	6b
Sources	Pliszka (1953)	Skora (1964)	Kennedy (1970)	Prejs (1973)	O'Maoileidigh (1989)	Giles (1990)	
Countries	**POLAND**	**POLAND**	**IRELAND**	**POLAND**	**IRELAND**	**G B**	
Sites (lake/river)	l. Harsz	l. Goczalkowice	several lakes	l. Warniak	l. Lough Leane	l. St Peter	l. Main
Sampling dates	V-XII (49-51)	III/VIII (61)	V-VIII (65-67)	IV-XI (67-69)	VI-IX (86)	V-VII (86-87)	
Nb stomachs examined	68 (1)	40	78 (2)	624	107	108	66
Nb of full stomachs	68*	40	52	487	62	108*	66*

* Authors did not mention the number of empty stomachs

Study number	1	2	3	4	5	6b	5	6a	1	4
Methods	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Occ.	% Num.	% Num.	% Weight	% Weight
Chironomids (l/p)	16.7	75	57.7	94	52.6		1.6	20.5		18.7
other Dipterans (l/p)			15.4	47.8*	12.1*					
Epheméropterans (l/p)		75	15.4	75						4
Trichopterans (l/p)	25	75	34.6	89	14.5		0.2	2.2	4.4	24
Coleopterans (l/a)	5		1.9	6	21		0.3		0.3	
Megalopterans (l/p)				8				2.9		
Heteropterans (a)			17.3	1						
Odonatans (l)				50						
Terrestrial insects			1.9	25	9.6					
Total insects	**39.7**	**100***	**87.4***	**100***	**75.3***		**2.14**	**25.6**	**4.7**	**46.7**
Amphipods			3.8		3.2			38.2		
Isopods	91.7		17.3	5	3.2			16.6	70	
Cladocerans		60	51	62	95.2	95	70.7			
Copepods			25	62	48.4		6.6			
Ostracods	6.7	75	21.1	71	43.5		12			
Total crustaceans	**91.8**	**85.1***	**78.6***	**98***	**100**	**95**	**89.34**	**54.8**	**70**	**15**
Diatoms		100								
Algae		75	21.1	91						
Macrophytes	16.7	75	17.3	90					1	
Total plants	**16.7**	**100**	**33.5***	**99***					**1**	
Teleosts				2						
Oligochets				70						
Molluscs	33.3	75	21	64	35.8		8.2	19.9	24	

(l/p) larvae and/or pupae; (l/a) larvae and/or adults; (a) adults, (l) larvae

*approximated % of occurrence

(1) 19 cm < individuals < 53 cm; (2) individuals > 14.5 cm

Aquatic plant matter, ingested mainly in summer and autumn (Prejs, 1973) is present in most stomach contents (Skora, 1964b; Prejs, 1973) but in reduced quantities (Kennedy and Fitzmaurice, 1970; Prejs, 1973; O'Maoileidigh and Bracken, 1989). Kennedy and Fitzmaurice (1970) supposed that aquatic plant matter ingested by tench was more probably accidental than deliberate and was the result of ingesting macroinvertebrates mixed with vegetation. On the other hand, Skora (1964b) observed very large aquatic plant masses in stomach contents; 32 to 58% of the total weight of food. Tench appears to be in direct competition with carp (Schaperclaus, 1962).

The loach (*Barbatula barbatula* L.) (Table XII)

Throughout the year the loach's basic food is made up of dipteran larvae, mostly chironomids (Hartley, 1947; Smyly, 1955; Maitland, 1965; Perrin, 1980). The latter are actively predated even though the loach is opportunist (Sauvonsaari, 1971). Among the aquatic insect group, other prey which are predominant, especially in spring and summer are ephemeropterans, plecopterans and particularly trichopterans. These can even become the loach's principal source of food (Sauvonsaari, 1971).

Benthic crustaceans, amphipods and isopods are commonly consumed and in autumn and winter can replace aquatic insects in the diet (Smyly, 1955; Welton, 1983).

An original feature of the loach's behaviour compared with other benthic fish is the large quantity of entomostracae which it ingests. Cladocerans and copepods are found in a large number of stomachs (Maitland, 1965; Sauvonsaari, 1971; Perrin, 1980; Welton, 1983). This is explained by the loach's preference for coastal zone grassy habitats (Welton, 1983), a preference distinguishing it from the bullhead which, in spite of a similar life style, inhabits more stony environments.

Depending on the trophic context, oligochaets are either the principal source of food (Welton, 1983) or totally absent from the diet (Perrin, 1980). This taxon is present mainly in autumn and winter (Smyly, 1955; Maitland, 1965; Welton, 1983).

As for occasional food, Sauvonsaari (1971) observed fish eggs and planktonic algae in a few specimens. Aerial insects can temporarily make up a large part of the loach's diet (Nikolsky, 1963). The principal rivals of the loach are the trout, the minnow, the stickleback (*Gasterosteus aculeatus* L.) and the bullhead (*Cottus gobio* L.) (Hartley, 1948; Smyly, 1955).

The stickleback (*Gasterosteus aculeatus* L.) (Table XIII)

The stickleback can survive both in brackish water or fresh water, slow or fast running currents and adapts its feeding behavior to its environment. Its diet consists mainly of insects and crustaceans. In rivers, the stickleback often coexists with the loach, the minnow and the trout and uses approximately the same feeding strategies (Maitland, 1955).

Almost throughout the year 25% to 33% of the stickleback's diet is made up of dipteran larvae, especially chironomids (Hartley, 1948; Hynes, 1950; Maitland, 1965; Mann and Orr, 1969) and these as well as various ephemeropterans are the only aquatic insects ingested. Conversely these aquatic insects seem little sought after in lakes.

Zooplankton, essentially copepods, make up almost 33% of the stickleback's diet regardless of the environment (Blegvad, 1916; Hartley, 1948; Hynes, 1950). Only the study carried out by Hynes (1950) observed low quantities of zooplankton is stomach contents.

Ingestion of higher crustaceans differs; according to certain authors these organisms make up less than 1 or 2% of total diet (Hartley, 1948; Hynes, 1950; Mann and Orr, 1969) whereas other authors state that amphipods and isopods form almost half the stickleback's

Table XII. - Feeding habits of the adult loach (*Barbatula barbatula* L.), expressed as percentage occurrence, percentage number, percentage volume, percentage weight and percentage point.

Study number	1	2A	2B	3	4	5	6	6
Sources	Hartley (1948)	Smyly (1955)		Maitland (1965)	Sauvonsaari (1971)	Perrin (1979)	Neveu (1981b)	Welton (1983)
Country	G B	G B		G B	FINLAND	FRANCE	FRANCE	GB
Sites (lake/river)	r. Cam	r. tributary Windermere	l. Esthwaite Malham Tarn	r. Endrick	l. Päijänne & Pälkänevesi	r. Rhône	r. la Nivelle	r. Frome
Sampling dates	I-XII (39-41)	VII- VIII				II-XII (76-78)	VI (76)	I-XII (80-81)
Nb stomachs examined	16	58	39	305	351	83(1)	63(2)	188 (3)
Nb of full stomachs	16*	58*	39*	305*	351*	83*	63*	188*

* Authors did not mention the number of empty stomachs

Study number	1	3	4	5	7	1	2A	2B	3	6	7	4	5
Methods	**% Occ.**	**% Occ.**	**% Occ.**	**% Occ.**	**% Occ.**	**% Num.**	**% Num.**	**% Num.**	**% Num.**	**% Num.**	**% Num.**	**% Vol.**	**% Points**
Chironomids (l/p)	50	83.6*	83*	86.5	55.6	19.7	41	32.5	44	35.2	5.2	15	41
Simuliids (l/p)	25	62.6*			12.3	30.8	8.9		7	28.2	1.5		
other Dipterans (l/p)	11.6*	64.1*	26.6	10.8					15			6.6	12
Ephemeropterans (l/p)	22.5*	52.6*	40.3	2.7		7.4	28.3	2	15	36.2		14.6	6.6
Trichopterans (l/p)	17.6*	15.6*	77.2	10.8	11.1	6.2	1.7	13	3		0.7	35.3	8.6
Plecopterans (l/p)		54.4*	0.9		22.2		15.5	8.5	9.5		2.2	0.5	
Coleopterans (l/a)		3*	12.9		33.3				<0.5		2.9	3.1	
Terrestrial insects (a)		5.7*					1.5		<1				
Total insects	**81.2**	**98.6***	**97.3***	**87.8***	**84.4***	**69.1**	**86.5**	**56**	**93.8**	**99.6**	**11**	**75.1**	**68..2**
Amphipods	18.7	28		35.1	11.1	21	2.4	6	3	0.4	0.7		31
Isopods			15.2		66.7						16.9	3.6	
Cladocerans	18.7		59.3	18.9	55.6	6.1	1.4	17.5	6.1		7.4	6.3	
Copepods	6.2	1	52.7		66.7	2.4			<0.5		10.3	0.5	1
Ostracods			18.1									0.1	
Total crustaceans	**43.7**	**29**	**87.5***	**45.8***	**100***	**29.6**	**3.8**	**23.5**	**9.2**		**35.7**	**10.5**	**32**
Fish eggs			6.4									1.5	
Molluscs			17.8		11.1			6			0.7	6	
Oligochets		7	11		100				<0.5		50	0.5	
Hirudineans			7.6				2.4					4.6	

(l/p) larvae and/or pupae; (l/a) larvae and/or adults; (a) adults; (l) larvae

*approximated % of occurrence

(1) 6 cm < individuals < 9 cm; (2) 4.8 cm < individuals < 8.9 cm; (3) adult fish

Table XIII. - Feeding habits of the adult stickleback (*Gasterosteus aculeatus* L.), expressed as percentage occurrence, percentage number, percentage volume and percentage point.

Study number	1	2	3a	3b	3c	4	5	6
Sources	Blegvad (1917)	Hartley (1948)	Hynes (1950)			Mann (1969)	Kislalioglu (1977)	Adalsteinsson (1979)
Countries	DENMARK	G B	G B			GB	GB	ICELAND
Sites (lake/river)	r.Brackish	r. Cam	r. Birket	l. Windermere	l. Easdale	r. Bere	l. Etive	l. Myvatn
Sampling dates		I-XII (39-41)	I-XII	I-XII		I-XII	I-XII (71-72)	VI-X (72-73)
Nb stomachs examined	427 (3)	227	1015	120 (2)	55	181	360 (4)	345 (5)
Nb of full stomachs	427*	227*	953	112	49	181*	360*	184

* Authors did not mention the number of empty stomachs

Study number	2	3a	3b	3c	2	4	5	3a	3b	3c	1	6
Methods	% Occ.	% Occ. (1)	% Occ.	% Occ.	% Num.	% Num.	% Num.	% Points (6)	% Points	% Points	% Weight	% Vol.
Chironomids (l/p)	42	17.3*	10.7	6.7	45.8	40.6		22.2	8	3		50.9
Simuliids (l/p)	1.8			6.7	0.9	22.3				4		
Ephemeropterans (l/p)	9				5.1	18.3						
Trichopterans (l/p)	1	1			0.3	0.5		1.7	2			
Terrestrial insects		2.6		7.8						4		8.7
Total insects	**66**	**20***	**10.7**	**19.2***	**51.3**	**81.7**	**21**	**27.3**	**10**		**8**	**59.6**
Amphipods	0.9			20	0.5	0.8-0.5	19	14.2	3	73	41	
Isopods	0.4	7.4	2	36								
Cladocerans	6.1	12.8	38.6		5.2		16	6.6	32		10	15
Copepods	23.8	21.3	32.1	4.5	32.2		10	14.5	40	5	27	15.1
Ostracods	3.5	7.4	13.9		3.6			2.8	7		1	
Total crustaceans	**30.4**	**41***	**64.4***	**49.8***	**41.3**			**38.1**	**82**		**79**	**30.1**
Diatoms	10.1	2										
Algae	18	5.3		3.3						3		
Macrophytes		3		6.7				2.2		2		
Total plants	**25.6**	**9.7***		**9.5***								
Fish eggs		1		4.5				2.58		2	8	3.2
Molluscs	3				1	2.1					1	5.7
Oligochets	0.4	6	4.3		0.3			12.4	6			
Detritus		3		1.1						1		2.5

(l/p) larvae and/or pupae; (l/a) larvae and/or adults; (a) adults; (l) larvae

*approximated % of occurrence

(1) 0.6 cm < individuals < 7.3 cm; (2) 2.1 < individuals < 5.3; (3) 0.5 cm < individuals < 11 cm; (4) 1.6 < individuals < 8.3; (5) average length: 8 cm; (6) 3 cm < individuals < 7.3 cm

diet (Blegvad, 1916; Hynes, 1950). These organisms are the preferred food of adult fish during winter (Hartley, 1948; Hynes, 1950).

Under certain circumstances, the stickleback has a herbivorous diet. Large quantities of diatoms were found in the stomach contents of adult fish (Saunders, 1914) and in September could make up 20% of total diet (Hynes, 1950). Hartley (1948) discovered filamentous algae in almost 20% of all fish caught.

The stickleback is reputed for its voracity and predatory behaviour towards the eggs of other fish (Blegvad, 1916; Bertin, 1925; Heiborn, 1931; Fisher, 1948; Hynes, 1950). This is one of the few fish which feeds on fish eggs even though eggs do not make up a large part of total diet. Blegvad (1917), however observed that up to 8% of total food ingested consisted of eggs.

The perch (*Perca fluviatilis* L.) (Table XIV)

The perch's diet is based largely on four groups of organisms: zooplankton, chironomids, higher crustaceans and fish. In most cases these prey make up the perch's diet and food item increases in size as the fish grows (Allen, 1935; Swynnerton and Worthington, 1940; Boikova, 1986).

Zooplankton is the basic food of young perch but surprisingly also makes up a large part of the adult's diet (Chikova, 1970; McCormak, 1970; Boikova, 1986). Forty three percent of specimens 16-18 cm long can still consume zooplankton, but over 18 cm the fish quickly abandon this type of food (McCormak, 1970). However Chikova (1970) observed a few 25 cm specimens containing up to 63% zooplankton of the total weight of ingested prey. Ingestion of zooplankton reaches a maximum in summer and the beginning of autumn (Chikova, 1970; McCormak, 1970; Boikova, 1986) sometimes spring (Persson, 1983b).

Chironomids are the only aquatic insects ingested systematically in all habitats, except in the study carried out by Mann (1978). They are rarely the principal food of adult perch except in certain habitats where they are abundant (Persson, 1983b; Chapaz *et al.*, 1989; Giles *et al.*, 1990) but often make up 20 -25% of diet (Craig, 1978; Boikova, 1986). Ephemeropterans, second most often consumed taxon in this group, is only mentioned in six out of thirteen papers and made up an exceptional 30% of total diet in the studies of Swynnerton and Worthington (1940), Shafi (1969) and Chapaz *et al.* (1989).

Ingestion of isopods and amphipods is very variable and depends on the environment. Sometimes they are totally absent or very few (Swynnerton and Worthington, 1940; Chikova, 1970; Mann, 1978; Persson, 1983b; Boikova, 1986) or make up the major part of the perch's diet (McCormak, 1970; Thorpe, 1977; Craig, 1978; Tugarina, 1974). In the same manner, considering all papers, no constant in seasonal ingestion of crustaceans was found.

Fish, however, represent nearly 50% of the diet of adult perch (Swynnerton and Worthington, 1940; Chikova, 1970; Mann, 1978); Goldspink and Goodwin, 1979; Boikova, 1986) which can therefore be considered piscivorous with benthophagous tendencies. Only older specimens, > 25 cm, have a strictly piscivorous diet (Swynnerton and Worthington, 1940; Chikova, 1970).

The change in diet takes place at > 11 cm according to Chikova (1970), at > 15 cm according to Shamardina (1967) or at > 16 cm according to McCormak (1970). Younger fish readily attack other fish (Krivobok, 1942; Mann, 1978; Chapaz *et al.*, 1989).

Cannibalism amongst perch populations, as observed by Alm (1946), Nikolski (1963) and Holsik (1967), is often high and can be attributed to concentrations of fry (Chikova, 1970). This type of predation by adult fish is not systematic (McCormak, 1970). This piscivorous diet becomes more accentuated during the summer period and especially in

Table XIV a, b. - Feeding habits of the adult perch (*Perca fluviatilis* L.), expressed as percentage occurrence, percentage number, percentage weight and percentage point.

Study number	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Sources	Mc Cormack (1970)	Chikova (1970)	Tugarina (1972)	Thorpe (1977)	Craig (1978)	Persson (1983)	Boikova (1986)	Chapaz (1989)
Countries	**G B**	**C.I.S.**	**C.I.S.**	**G B**	**G B**	**SWEDEN**	**C.I.S.**	**FRANCE**
Sites (lake/river)	I. Windermere	I. Kuybyshev	I. Gusinoye	I. Leven	I. Windermere	I. Sövdeborgssjön	I. Glubokoe	I. Sainte-Croix
Sampling dates	VI-IX	IV-X	V-X (64-67)	VI-IX	I-XII	IV-XI (80)	V-VI	XII-III/VIII (84-85)
Nb stomachs examined	637 (2)	42 (3)	616 (6)	1116	1148		54 (5)	6 7
Nb of full stomachs	387	4 2	61 6*	1116*	1148*		54*	6 7*

* Authors did not mention the number of empty stomachs

Study number	**1**	**3**	**5**	**7**	**8**	**2**	**3**	**4**	**6**	**7**
Methods	**% Occ.**	**% Occ.**	**% Occ.**	**% Occ.**	**% Occ.**	**% Weight**	**% Weight**	**% Weight**	**% Weight**	**% Weight**
Chironomids (l/p)	12.8	28.7	30.3*	38.8	53.8	0.8	23.4	13.1	66	9.1
Other Dipterans (l/p)					29.5					
Ephemeropterans (l/p)	2.6				34					
Trichopterans (l/p)	0.6				12.3				8.7	
Coleopterans (l/a)					3.8					
Megalopterans (l/p)			6.1							
Heteropterans (a)					9.3					
Odonatans (l)				24.1	8.7					12.2
Total insects	**15.4***	**28.7**	**34.1***	**51.6***	**90.4***	**0.8**	**23.4**	**13.1**	**80.7**	**21.3**
Decapods					3.8					
Amphipods	24.6	70	13.8		13		20.6	6.1	1.1	
Isopods	28.5		15.5		3.6			33.8	2.8	
Cladocerans	8.2	22.5	36.1	16.8	5.9	49.2	2.5	14.6		
Copepods				22	5.9				1.5	
Ostracods					2					
Total crustaceans	**49.5***	**74.6***	**52.4***	**38.8***	**30***	**49.2**	**23.1**	**54.5**	**5.4**	**3.1**
Cottus gobio	0.7									
Phoxinus phoxinus	7.1									
Perca fluviatilis	7.1	71.2	17.4			32.6	46.9	13.5		
Other teleosts		8.7				15.6				
Total teleosts	**13.8***	**72.8***	**17.4**	**32.2**	**26.9**	**47.2**	**49.3**	**13.5**	**2**	**69.3**
Oligochets					0.2				2.5	
Hirudineans	6.3							12.9		
Molluscs		30								

(l/p) larvae and/or pupae; (l/a) larvae and/or adults; (a) adults; (l) larvae

*approximated % of occurrence

(1) individuals > 20 cm; (2) individuals > 18.5 cm; (3) individuals > 18 cm; (4) individuals > 20 cm; (5) 15.7 < individuals < 25.6 cm; (6) individuals > 3+

Table XIV b.

Study number	1	2a	2b	3	4	5
Sources	Swynnerton (1940)	Shafi (1969)		Mann (1978)	Goldspink (1979)	Giles (1990)
Countries	GB	G B		G B	G B	G B
Sites (lake/river)	l. Haweswater	l. Duhh	l. Lomond	r. Stour	l. Rostherne	l. Main & St Peters
Sampling dates	VII			I-XII (68-74)		V-VII (86-87)
Nb stomachs examined	17 (1)			47 (4)	821	182
Nb of full stomachs	13			38	821*	182*

* Authors did not mention the number of empty stomachs

Study number	1	2a	2b	3	5	4
Methods	% Num.	% Num.	% Num.	% Num.	% Num.	% Points
Chironomids (l/p)	13.6	12.1	14.3		65	14.5
Ephemeropterans (l/p)	29.6	30.4	3.2	5.4	4.9	
Trichopterans (l/p)		0.7	1.6	1.6		1.7
Heteropterans (a)				26.4	11.6	
Odonatans (l)				4.7	1.5	
Total insects	**43.2**	**43.2**	**19.1**	**38.1**	**83**	**16.2**
Decapods						
Amphipods	1.6			3.1	11.3	
Isopods					5.8	
Cladocerans	1.6	36.6	7			6
Copepods		11.9	42.1			1.7
Total crustaceans	**3.2**	**48.5**	**49.1**	**5.4**	**17.1**	**7.7**
Cottus gobio				4.7		1
Phoxinus phoxinus				27.8		
Perca fluviatilis		0.1				25.5
Other teleosts				20.9		
Total teleosts	**48.8**	**0.1**	**7.2**	**53.4**		**39.6**
Hirudineans						1.9
Algae	3.2					2.5
Detritus	1.6					

(l/p) larvae and/or pupae; (l/a) larvae and/or adults; (a) adults; (l) larvae

(1) individuals > 20 cm; (4) individuals > 19.9 cm

autumn (McCormak, 1970; Craig, 1978; Goldspink and Goodwin, 1979; Chapaz *et al.*, 1989).

Perch can occasionally feeds on macrophytes. Mann (1978) found these organisms in 16% of specimens of 10-20 cm and even in 4% > 20 cm.

In general most prey are ingested in summer, although surprisingly McCormak (1970) observed 62% of specimens with empty stomach contents during August. Finally, this species of fish can ingest up to 6.5% of its own weight per day during June (Thorpe, 1977).

The bullhead (*Cottus gobio* L.) (Table XV)

The bullhead's diet is made up exclusively of insects and benthic crustaceans. Among insects, chironomids represent a predominant 40% of the bullhead's food (Hartley, 1948; Mann and Orr, 1969; Paschalski, 1959; Andreasson, 1971; Abel, 1973). Andreasson (1971) illustrated that bullhead ingest larger and larger quantities of chironomids during their growing period, reaching a maximum proportion of food ingested at 7.5 cm in length. Above this size, the quantity of chironomids in the diet decreased to be gradually replaced by larger prey such as trichopterans.

Smyly (1957) observed that lake bullhead ingested larger quantities of trichopterans and benthic crustaceans (especially *Gammarus*) than river bullhead. According to most work carried out on this species these two taxons are the bullhead's second most preferred food resource after chironomids (Hartley, 1948; Morris, 1965; Andreasson, 1971; Welton,

Table XV. - Feeding habits of the adult bullhead (*Cottus gobio* L.), expressed as percentage occurrence, percentage number, percentage weight and percentage volume.

Study number	1	2a	2b	3	4	6	7	8	9	1 0		1 1	13
Sources	Hartley (1948)	Smyly (1957)		Paschalski (1958)	Crisp (1983)	Morris (1963)	Morris (1965)	Cihar (1954)	Mann (1969)	Andreasson (1971)		Zelinka (1971)	Welton (1983)
Countries	**G B**	**G B**		**POLAND**	**GB**	**G B**	**G B**	**CZECHOSLOVAKIA**	**GB**	**NORWAY**		**CZECHOSLOVAKIA**	**GB**
Sites (lake/river)	r. Cam	r. Brathay	l. Windermere	r. Poroniec	r. Tees	r. Willow Brook	r. Afon Llafar	r. Moravka	r. Bere	r. Trydea		r.?	r. Frome
Sampling dates	I-XII (39-41)	I-XII (51-54)			IV-VIII (60)	I-XII	I-XII		I-XII	I-XII			I-XII (80-81)
Nbstomachs examined	8 4	771	1555	5 0 (1)	72			93 (1)(2)	1125 (3)	21	10		99
Nb of full stomachs	8 4*	362	1089	4 7	55			93 *	1125*	21	10*		99*

* Authors did not mention the number of empty stomachs

Study number	1	3	4	11	1	3	5	8	9	10	10 (1)	12	2a	2b	6	7	5
Methods	% Occ.	% Occ.	% Occ.	% Occ.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% Num.	% vol.	% vol.	% Vol.	% Vol.	% weight (4)
Chironomids (l/p)	21.4	90	42	12.9	38.5	74.6	76.2	50	23.5	20	68	3.3	4	2	6	7	2.7
Simuliids (l/p)	4.8		7	2	2.7		0.7	5	10.2	1	1	0.3			4		1.5
Other Dipterans (l/p)	9*	16			6.6	3.7	0.9										
Ephemeropterans (l/p)	10.7	38	22	8.3	6	4.4	3.9	10	15.5	33	11	3.2	16	17		10	14.5
Trichopterans (l/p)	13.1	72	24	16.4	9.3	8.3	10.2	16	8.3	25	11	4.5	5	13	17	15	36.9
Plecopterans (l/p)		48	33			4.9	1.3	19		5	5		21	17		8	8.3
Coleopterans (l/a)	3.6*	26	3	3.6	1.6	2.1	0.7					1.8					
Megalopterans (l/p)	8.3				4.9									3			
Terrestrial insects			6.6														0
Total insects	**69**	**94***	**89***	**36.9***	**69.6**	**98**	**93.9**	**100**	**57.5**	**84**	**96**	**13.1**	**46**	**52**			
Decapods	3.6																
Amphipods	40.5			18.8	22		5.3		15.2	5	2	3.9	1	17	26		36.2
Isopods	3.5			89.1	4.4		0.1		5.5			66.9			19		
Copepods	1.2			12.5	0.5							3.5					
Ostracods				0.7			0.2					4					
Total crustaceans	**46.4**			**90***	**26.4**		**5.6**		**20.7**			**78.3**		**17**			**38.2**
Teleosts		14	3			1.1	0.1										2.3
Molluscs	1.2			13.7					5.9			4.6	2	1		6	
Oligochets	3.6			3.6								1.1				21	
Algae		6				0.5											

(l/p) larvae and/or pupae; (l/a) larvae and/or adults; (a) adults; (l) larvae

*approximated % of occurrence

(1) species: Cottus poecilopus; (2) 4.2 cm < individuals < 11.2; (3) individuals > 4 cm; (4) individuals > 5.3 cm

1983). Together they make up 20% (numerical abundance) of the diet and represent the largest dietary biomass especially for older fish (Andreasson, 1971). Ephemeropterans and plecopterans follow in respective order of importance. Crustaceans appear to be ingested mainly in winter (Welton, 1983) whereas aquatic insects are predominant in the diet at the end of spring and in summer (Andreasson, 1964; Morris, 1965; Smyly, 1957).

Work on the trophic competition between trout and bullhead (Müller, 1952; Brocksen *et al.,* 1968; Mann and Orr, 1969; Andreasson, 1971; Crisp, 1983) showed that in spring, the diet of bullhead is similar to that of young trout but differs progressively in summer and especially in autumn once aerial insects, the preferred diet of trout, become abundant. Hartley (1948) suggested that stickleback and gudgeon are in direct competition with bullhead for chironomids.

As to the incidental predation of bullhead on salmonid eggs and fingerlings, this appears to be rare or accidental, as the bullhead prefers mobile prey (Smyly, 1957).

Analysis of feeding groups

The first three axes of the factorial analysis (Fig. 2a, b) performed on the Food Items-by-Fauna matrix (Table XVI) explained 68.7 % of the overall variability. Axis 1 (32.35% contribution) (Fig. 2a) clearly separated the invertivorous species from all the others. We used the general term "invertivorous species", because these fish typically eat crustaceans, molluscs, and oligochaets, as well as insects. The second axis (22.38% contribution) (Fig. 2a) distinguished a more restricted number of species and separated omnivorous species (omnivorous species being defined as species that consistently feed on substantial proportions of plant and animal material) in two distinct groups reflecting differences in feeding tendencies: omnivores with zooplanktivorous tendencies and omnivores with herbivorous-detritivorous tendencies. Axis 3 (13.93% contribution) (Fig. 2b) isolated species with piscivorous tendencies. Remaining axes did not provide useful dietary informations.

Four distinct clusters were recognized in the trophic dendrogram (Fig. 2c). Cluster 1 depicted a small group of species which feed exclusively upon invertebrate material. These species were classified as invertivores (*Salmo trutta*, *Anguilla anguilla*, *Cottus gobio* and *Barbatula barbatula*). Cluster 2 was the largest of the dendrogram and depicted species which feed upon both invertebrate and plant material. These species were classified as omnivores. Cluster 2 was subdivided into two groups. The upper was composed of three cyprinids with herbivorous-detritivorous tendencies (*Phoxinus phoxinus*, *Leuciscus leuciscus* and *Rutilus rutilus*). The lower group of cluster 2 was composed of one gasterosteid and four cyprinids with zooplanktivorous tendencies (*Gasterosteus aculeatus*, *Cyprinus carpio*, *Gobio gobio*, *Tinca tinca* and *Abramis brama*). Clusters 3 and 4 each contained a single species and depicted an omnivore species with piscivorous tendencies (*Leuciscus cephalus*; cluster 3) and a piscivorous species (*Perca fluviatilis*; cluster 4).

CONCLUSION

Our specific goal before starting this research was, compiling previous published data, to classify all freshwater fish species living in West European rivers by their food habits. Unfortunately, very few published studies were available for most of the species and, consequently, we were obliged to limit our investigation to the fourteen most docu-

Table XVI. - Synthetic picture of the feeding habits of fourteen European freshwater fish species compiled from 89 studies. Results are given for each species in percentage of occurrence.

Prey items / Species	Eel		Brown trout		Bullhead	Minnow		Dace	Gudgeon		Chub	Tench	Carp	Bream		Roach		Loach		Stickleback		Perch
	riv.	lake	riv.	lake	riv.	riv.	lake	riv.	riv.	lake	riv.	lake	lake	riv.	lake	riv.	lake	riv.	lake	riv.	lake	lake
Chironomids	13.1	10.7	28.4	34.1	36.5	49.4	46.4	12.1	58.2	69	1	79.3	78.7	90	69.3	10.9	20	74.2	83	20.9	0.5	24.1
Simuliids	6.3	1.7	9.3	1.3	3.7	7.1		8.2	8.6		3.8					3		38.1		0.3	2	
Other Dipterans	1.6		10.3	4.7	5.7	13.4			8.6		0	33			8.2	1.5	1.6	34.5	26.6			
Ephemeropterans	27.7	20.8	39.2	22.6	17.8	19.2		4	8.9	7.4	0	57.3	26.3	31	9.6	1	4	28	40.3	1.7		1.4
Trichopterans	44.2	28.6	60.2	56.7	27.8	13	8.4	30	6.4		21.9	71.9	36.1	16	9.3	1.8	13.1	13.6	77.2	1.1		0.5
Plecopterans	20.2		32.3	10.4	8.5	7.6				4.5	3						1.6	33.9	0.9			
Terrestrial insects	0.9		59.4	52.6	1.3	22.7		6			16	16.5				3.5		3		2.1	2.5	
Amphipods	6.6	13.5	9.6	29.4	17.1	5.1	3.2	5.3	17		0	0.6	6.6		1.7	7.1	7.1	23.3		3.1	10.6	30.5
Isopods	3	13.5	7.3	11.3	25						0	12.9	1.6		5.2		3.8	21.1	15.2	3	10	12.8
Cladocerans				7.3		11.7	50.4		7.8	23.5	0	61.1	40.5	16	73.4		34.3	21.8	59.3	12.5	26.7	26.3
Copepods					3.7	7			8.4	12.6	0	49	24.7	26	41.6	0.6	25.5	21.9	52.7	25.8	23.7	0.7
Ostracods				0.5	0.2	1.2			3.6		0	59.3	21.7		14.7	2.1	9.5		18.1	7.3	9.7	
Teleosts	14.1	4	4.9	10	3.2	1.1					21.2	1.4	0.8									28.8
Molluscs	8.3	63	8.8	24.8	4	4.8	13.6	9.5	19.8	3.2	0	56.8	56.3	79	7.2	22.1	59.4	3.5	17.8	0.6		
Oligochaets	7.2	1.7	1.8	0.6		8.3				7.3	0	48.3	27.9		22.1		2.1	35.3	11	5.1	3	
Diatoms						23.5		11.7	0.5	7.4	11.1	6.2	5.3		16.5	3.6	17.3			3.7		
Algae	0.4			1.4	1	37.5	13.5	9	9.5	4	27.6	68.9	25.5		8.8	5.8	28.5			10.8	1	
Macrophytes						12.9		3			16.8	69.3	69.2	31	19.5	34	45.8			2.5	2	
Detritus						23			0.9	29.4	14.1		29.9		24.5	10.3	0.8			2.4	0.3	
Number of studies	10	3	12	4	4	3	1	1	2	2	1	6	6	1	7	2	10	4	1	2	2	5
Number of fish examined	2067	177	2428	1564	307	978	199	231	416	72	231	775	1398	44	2767	329	2263	592	351	1180	161	2522

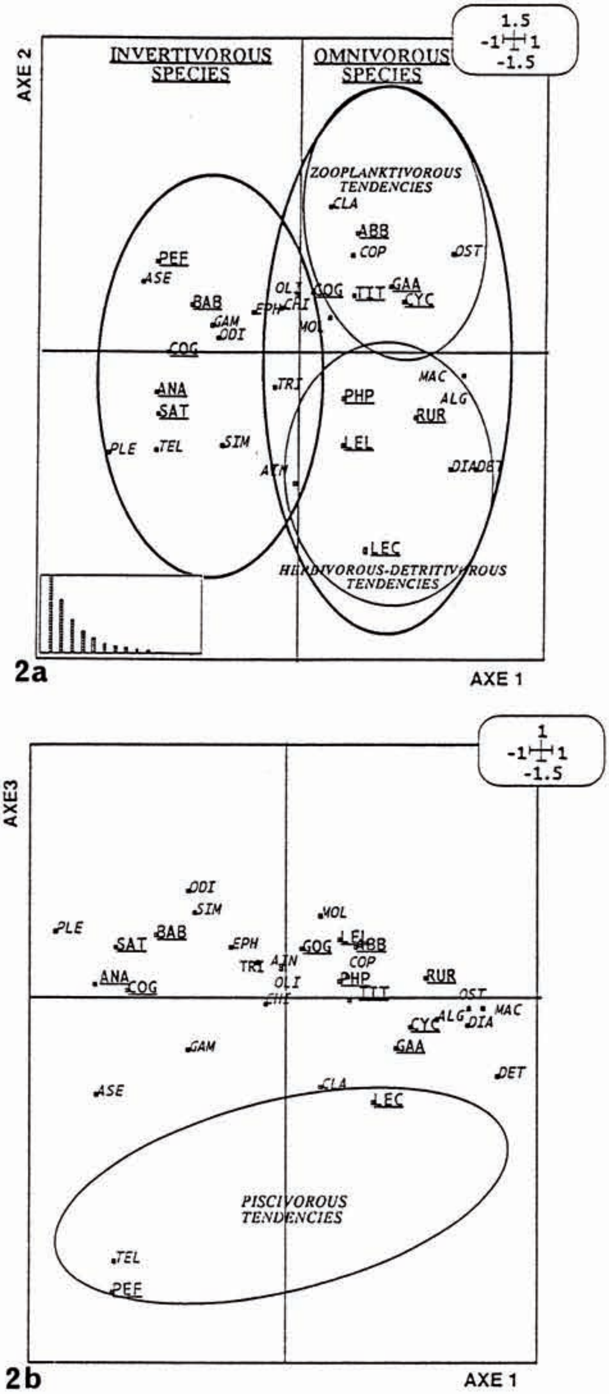

Fig. 2. - (a) Trends in feeding habits of fourteen freshwater fish as revealed by the first two axes of the correspondence analysis. (b) Trends in feeding habits of fourteen freshwater fish as revealed by the first and third axes of the correspondence analysis.

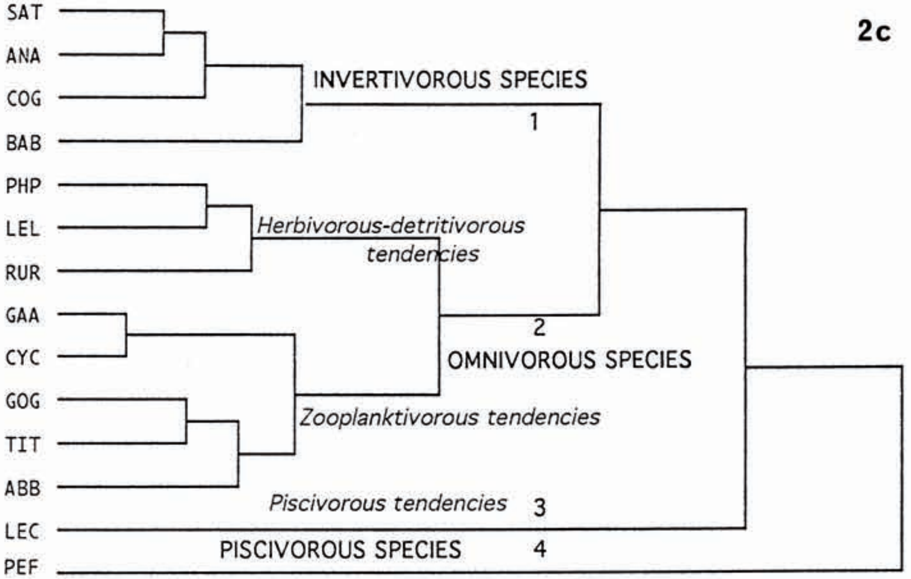

Fig. 2 (continued). - (c) UPGMA dendrogram showing trophic relationships between the fourteen species based upon the three first axes of the correspondence analysis. Codes for fish species and prey items are as follow: *Anguilla anguilla* (ANA), *Salmo trutta fario* (SAT), *Phoxinus phoxinus* (PHP), *Gobio gobio* (GOG), *Leuciscus leuciscus* (LEL), *Leuciscus cephalus* (LEC), *Abramis brama* (ABB), *Rutilus rutilus* (RUR), *Cyprinus carpio* (CYC), *Tinca tinca* (TIT), *Gasterosteus aculeatus* (GAA), *Barbatula barbatula* (BAB), *Perca fluviatilis* (PEF) and *Cottus gobio* (COG). Chironomids (CHI), simuliids (SIM), other dipterans (OTD), ephemeropterans (EPH), trichopterans (TRI), plecopterans (PLE), terrestrial insects (AEI), amphipods (AMP), isopods (ISO), cladocerans (CLA), copepods (COP), ostracods (OST), teleosts (TEL), molluscs (MOL), oligochaets (OLI), diatoms (DIA), algae (ALG), macrophytes (MAC), detritus (DET).

mented ones. Information found in the general litterature is based on data whose origins are not clear. To this extent, we must question the viability of such information. A more thorough research needs to be achieved if we want to extend this synthesis to other species.

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